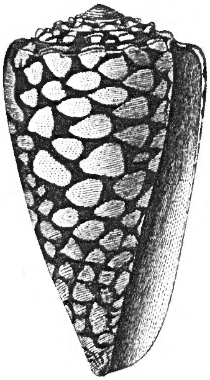

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Molluscan Research

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Ecology of the sea hare *Aplysia parvula* (Opisthobranchia) in New South Wales, Australia

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Abstract

The present study investigates the host range, distribution, abundance, activity and feeding preferences of the sea hare *Aplysia parvula* on the New South Wales (NSW) central and south coast. *Aplysia parvula* was found to occur mainly on red algae, especially *Delisea pulchra* and *Laurencia obtusa* near Sydney, NSW. The abundance of *A. parvula* was positively related to the abundance of *D. pulchra* and *L. obtusa* and sea hares were absent when survey sites lacked these algae. *Aplysia parvula* occurred in greater abundance on *L. obtusa* compared with *D. pulchra*, although *L. obtusa* is ephemeral near Sydney. Fluctuations in the abundance of *A. parvula* on *D. pulchra* suggest that *A. parvula* individuals persist for only a few months and are short lived. *Aplysia parvula* appears to prefer small *D. pulchra* plants with lower levels of secondary metabolites. The diet of *A. parvula* was not restricted to host algae, because animals consumed a range of co-occurring red, green and brown seaweeds. *Aplysia parvula* was nocturnally active on host algae; it grazes and copulates in the canopy of host algae at night, as well as moving between plants. *Aplysia parvula* may compete with other herbivores (notably *Aplysia dactylomela*) for the less-abundant *L. obtusa* resource. Interspecific competition appears less likely on *D. pulchra*, because few other sea hares were found on this seaweed.

Additional keywords: abundance, algal diet, consumption, diel activity, habitat choice, herbivore.

Introduction

A considerable body of literature exists on the neurophysiology and anatomy of sea hares. In comparison, relatively little is known of the natural history and ecology of these molluscs. Some studies have investigated the population ecology of sea hares (Sarver 1979; Gev *et al.* 1984; Pennings 1991*a*), whereas others have considered their activity patterns (Carefoot and Taylor 1988; Carefoot 1989, 1991; Pennings 1991*b*). The natural products of sea hares have been studied extensively (for a review, see Avila 1995), yet the ecological role of acquired secondary metabolites is still debated (e.g. Pennings and Paul 1993; Rogers *et al.* 2002).

Many authors have noted spatial and temporal variation in the abundance of sea hares (for a review, see Carefoot 1987) and sea hares are generally considered to be ephemeral in occurrence. Adult abundance is generally less than a few individuals per square metre, except for breeding aggregations (Carefoot 1987). Factors that influence the abundance of sea hares include physical processes that affect larval supply, survival of recruits and habitat suitability (Sarver 1979; Carefoot 1987; Pennings 1991*a*), the abundance of host algae as recruitment sites and food (Sarver 1979; Gev *et al.* 1984; Pennings 1991*a*) and biotic interactions, including predation and competition (Sarver 1979; Achituv and Susswein 1985; Pennings 1990*a*, 1990*b*; Pennings *et al.* 2001).

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Dispersal of planktonic larvae is thought to be the primary determinant of the distribution of sea hares (Sarver 1979; Pennings 1991*a*). Larval supply depends on the fecundity of source populations, biotic conditions affecting larval survival and physical oceanographic processes (Morgan 1995; Pechenik 1999). Sea hares with cosmopolitan distributions, such as *Aplysia parvula* (Guilding in Mörch, 1863), *A. juliana* (Quoy and Gaimard, 1832) and *A. dactylomela* (Rang, 1828) (Carefoot 1987), have resilient veliger larvae capable of prolonged existence in the plankton and widespread dispersal (e.g. Kempf 1981). Adverse physical conditions, including temperature, salinity, wave action, tidal cycles and ultraviolet radiation, can cause mortality in populations of both larval and benthic sea hares (Sarver 1979; Carefoot 1987).

Host algae (juvenile foods) are preferred sites of metamorphosis for larvae in most species of sea hare studied (Switzer-Dunlap 1978), although Pawlik (1989) found that recruitment was not limited to host algae in *A. californica* (Cooper, 1863). However, metamorphosis of *A. californica* veligers is highest on the host algae *Plocamium cartilagineum* ((Linnaeus) Dixon, 1967) and *Laurencia pacifica* (Kylin) and juvenile *A. californica* preferentially inhabit and grow best on these red seaweeds (Pennings 1990*c*). The abundance of *A. californica* was significantly linked to the abundance of *P. cartilagineum* within a site, but not between sites (Pennings 1990*c*, 1991*a*). Pennings (1991*a*) attributed differences in the abundance of *A. californica* between sites to physical oceanographic processes affecting larval supply. *Aplysia parvula* is most often found on red seaweeds and has been reported to occur on *Acanthophora spicifera* ((Vahl) Børgesen), *Asparagopsis taxiformis* ((Delile) Trevisan, 1845), *Laurencia* spp. (Lamouroux, 1813), *Plocamium costatum* (C. Agardh, 1822) and *Portieria* (*Chondrococcus*) *hornemannii* ((Lyngbye) Silva, 1987) (Morton and Miller 1968; Willan 1979; Switzer-Dunlap and Hadfield 1981; Carefoot 1989; Faulkner 1992). In the Sydney region, *Aplysia parvula* has been found on *Delisea pulchra* ((Greville) Montagne, 1844) and *Laurencia obtusa* ((Hudson) Lamouroux, 1813), which occur in different habitats, as well as on *L. rigida* (J. Agardh, 1876) and the green alga *Ulva* sp. (Linnaeus, 1753) (Rogers *et al.* 1995).

The abundance of sea hares is also affected by biotic interactions. Juvenile sea hares can be subject to high rates of predation that may significantly reduce their abundance (Pennings 1990*a*; Rogers *et al.* 2000, 2002; Ginsburg and Paul 2001; Pennings *et al.* 2001). In contrast, adult sea hares are thought to be free from most predators (Carefoot 1987; Pennings 1990*c*), although adult *A. parvula* are consumed by fishes (Rogers *et al.* 2002). Competition has rarely been investigated for sea hares. One study reported the possibility of niche separation between sympatric species (Achituv and Susswein 1985), whereas another suggested competition for *Laurencia* sp. between *A. parvula* and *A. dactylomela* (Willan 1979). Carefoot (1989) argued that food was not limiting in a separate study of *A. parvula* and *A. dactylomela*.

Early neurological studies of the aplysiid eye reported a circadian rhythm (Kandel 1979) and subsequent field studies of activity patterns in sea hares by Carefoot (1985, 1989, 1991) found distinct patterns of behaviour during the diel cycle. *Aplysia dactylomela* is nocturnal, becoming active at dusk and moving to find mates, copulating, then feeding during the early hours of the morning and resting during daylight hours (Carefoot 1985). This behaviour pattern was found to be consistent between populations of *A. dactylomela* in Hawaii and Jamaica (Carefoot 1989, 1991). The activity patterns of *A. fasciata* (Poiret), *A. parvula* and *A. californica* have also been studied. All three species are active during the day and at night (Susswein *et al.* 1983; Carefoot 1989; Pennings 1991*b*). These studies of sea hare activity mostly considered reproductive adult populations, although the *A. parvula* individuals

investigated by Carefoot (1989) were small (<1 g live weight). The activity patterns of juvenile sea hares may vary from those of adults because of the threat of predation.

Many opisthobranchs are specialised feeders, consuming only a few types of food (Karuso 1987; Faulkner 1992; Jensen 1997). However, most adult sea hares are an exception to this general pattern, foraging on a variety of red, brown and green algae, sea grasses and cyanobacteria, although *A. juliana* consumes Ulvales almost exclusively (Carefoot 1987; Gerwick and Whatley 1989; Paul and Pennings 1991). Juvenile sea hares have restricted diets, often limited to one or a few types of algae (Pennings 1990*c*). Sea hares generally consume macrophytes with soft tissues that they can bite easily and avoid toughened or calcified species (Carefoot 1987; Pennings and Paul 1992). Because specimens of *A. parvula* are small even as adults (typically <5 g wet weight (wt)), they use algae as both food and habitat during their benthic life (e.g. mesogazers; Brawley 1992; Paul *et al.* 2001), unlike other larger species that forage in the open. The objective of the present study was to describe the benthic phase of the life cycle of *A. parvula* in New South Wales (NSW), its host plants, abundance, activity patterns and dietary range.

Materials and methods

Study sites and determination of host algae

The main sites for field work were Astrolabe Cove, Congwong Bay, Bare Island and Cruwee Cove on the northern shores of Botany Bay and Shark Bay and Parsley Bay in Port Jackson, near Sydney (NSW, Australia). Surveys to determine which algae *Aplysia parvula* inhabit were conducted at these sites and those listed below using SCUBA. *Aplysia parvula* is most commonly reported on red algae, so all red macroalgae encountered during dives were searched for sea hares. When sea hares were located on an alga, part of the seaweed was collected for identification. Sites from Port Jackson (33°50S, 151°15E) south to Narooma (36°10′S, 150°5′E) were investigated for sea hares and red algae. Localities that were studied include: Hermit Point, Blackburn Cove, Mrs Macquarie's Point, Bradleys Head, Taylor's Bay, Chowder Head, George's Head, Sow and Pigs Reef and Vaucluse Bay, all of which are in Port Jackson; Kurnell and Silver Beach on the southern shores of Botany Bay; Shelly Point, Bass and Flinder's Point at Port Hacking; Kiama; Hyam's Beach and Murray's Beach in Jervis Bay; Summercloud Bay; Kioloa; and Josh's Beach and South Brou Beach near Narooma.

Field surveys of Aplysia parvula *and host algae*

The distribution and abundance of *Aplysia parvula* and algae were studied at three sites (Congwong Bay, Cruwee Cove and Shark Bay) from April 1995 to July 1997. These sites were chosen based on the presence of the host algae *Delisea pulchra* or *Laurencia obtusa*, within the mixed algal communities at each site. The sites were located on sandstone reefs and varied in depth from 1 to 3 m below spring low water. Each survey area consisted of a 100-m^2 patch bordered by markers spaced at 10 m on the north side and on the east or west sides. Surveys were conducted on SCUBA using a grid system to randomly locate quadrats for measuring algal cover or transects to measure sea hare abundance. Quadrats consisted of a square steel frame covered with mesh (10 × 10 grid) to measure percentage algal cover using the point intercept method. For each sampling event, 10 replicate 0.25-m^2 quadrats were measured. Replication and quadrat size (0.25 m^2) were chosen to determine patterns of algal abundance at each site within the time constraints imposed by diving. Transects were used to determine sea hare abundance because these molluscs occurred at low abundance and were widely scattered among the seaweeds. Five replicate 4 × 0.5-m (2-m^2) transects were sampled by searching the substrata and all seaweeds for sea hares. Bottom water temperature (in °C) was recorded at each site during surveys using a digital depth gauge (Scubapro-Uwatec, Sydney, Australia). Surveys were conducted at 2-monthly intervals when possible. Because *A. parvula* is cryptic on host algae, search efficiency was evaluated in three replicate transects in a *D. pulchra* patch at Cruwee Cove on 25 October 1994. All *A. parvula* individuals were counted using transects as described above, then the *D. pulchra* plants were collected from each transect, taken to the laboratory and examined for sea hares. The number of sea hares counted in the field was then divided by the number found on algae in the laboratory to obtain a value for search efficiency. The mean (± s.e.m.) number of sea hares found during field transects

was 64.9 ± 19.1%; hence, search efficiency was high, but juvenile sea hares were often overlooked because they are small and highly cryptic.

Collections of *D. pulchra* and *L. obtusa* were also made during the present study to measure sea hare abundance at Bare Island and Shark Bay. All collections of algae were performed haphazardly in algal patches of generally less than 50 m^2. Algae were placed into individual plastic bags *in situ*, then taken to the laboratory to measure sea hare abundance and the wet weight of algae. No collections of algae or sea hares were made within or near fixed survey sites.

Assessment of factors that correlate with sea hare abundance on Delisea pulchra

To investigate various factors that may influence the abundance of *Aplysia parvula* (i.e. abundance of other herbivores, plant physical characteristics or levels of secondary metabolites), collections of *Delisea pulchra* and associated epifauna were taken at Astrolabe Cove on 5 and 13 July 1995 in two areas approximately 100 m apart. The close proximity of sample areas minimised the possibility of effects resulting from differences in physical conditions. Plants were collected haphazardly from patches in each area, which were on sandstone reefs at 2–3 m depth and differed in their abundance of *A. parvula* (they appeared absent at one area), but were otherwise similar in most respects. Most of the *D. pulchra* collected had some epibionts, including encrusting coralline algae, *Ulva* sp., *Enteromorpha* sp., *Colpomenia* sp., filamentous red or brown algae and sponges. The apices of the *D. pulchra* collected were not bleached (bleaching of apices occurs during summer; C. N. Rogers, unpublished observation). Thirty plants were collected haphazardly from the algal beds (approximately 50 m^2 in size) in each area and placed in individual plastic bags with 2–3 L sea water. In the laboratory, each plant was searched and the numbers of *A. parvula*, the gastropods *Phasianotrochus eximius* (Perry, 1811) and *Dentimitrella lincolnensis* (Reeve, 1859) and the sea urchin *Holopneustes purpurescens* (Agassiz, 1872) were recorded. These species were the most abundant herbivores found on *D. pulchra*. Other epifauna included decorator crabs (*Naxia* sp.), Ophiuroidea, dorid and aeolid nudibranchs and errant and sedentary polychaete worms; data for these less abundant epifauna are not presented here. Physical data for each plant were also recorded, including wet weight (wt), length from holdfast to apices and breadth at canopy, then each plant was frozen for chemical analysis. Whole *D. pulchra* plants were freeze-dried, ground to powder and 200 mg was then extracted using 5 × 5 mL aliquots of 100% analytical grade dichloromethane. Samples were quantitatively analysed for secondary metabolites using gas chromatography–mass spectrometry following the methods of de Nys *et al.* (1996). Two additional measures of the physical characteristics of *D. pulchra* plants were also calculated. The first was emersed plant volume, which was calculated using the formula for the volume of a cone (because *D. pulchra* often has a conical habit at shallow depths). The second was plant density, which was calculated by dividing plant wet wt by volume. This measure gives an indication of the packing of algal thalli, bulky plants having more thalli per unit volume (higher density) compared to plants with sparse thalli.

Activity patterns of Aplysia parvula

The activity patterns of *Aplysia parvula* were recorded *in situ* using SCUBA to observe sea hares on 15 tagged *Delisea pulchra* plants. Tags were relocated if sea hares moved from marked plants. The activity of sea hares was classified into four categories, which are (in order of decreasing energetic requirement) as follows: moving, grazing, copulating and resting (Carefoot 1989). Where sea hares were engaged in more than one activity (e.g. grazing and copulating), these were recorded, although only the most energetic activity is presented for each individual (i.e. one individual as grazing and the second sea hare as copulating). Dives to record activity were staggered over consecutive weeks, each being separated by at least 12 h because activity may not be independent during shorter periods (Pennings 1991*b*). Activity was observed for eight different time periods during November 1998. The activity patterns of *A. parvula* on *Laurencia obtusa* were observed during a separate study of sea hare movements (Rogers *et al.* 1998). Observations at night were made using torches to illuminate plants and typically lasted less than 1 min. *Aplysia parvula* often moves between algae after being illuminated at night (Rogers 1999); however, this behaviour did not affect determination of activity patterns because this movement occurred after observations were made. When animals were not visible on tagged plants, thalli were parted and searched to locate sea hares.

Dietary range of Aplysia parvula

The dietary range of *Aplysia parvula* was assessed in a no-choice consumption experiment that included the host plant *Delisea pulchra* and co-occurring red, green and brown algae. Individual *A. parvula* were weighed (mean size 0.554 ± 0.019 g wet wt) and then placed into separate cells of 25-L experimental

aquaria (divided into 20 cells per aquarium) supplied with flowing seawater. Five replicate sea hares were offered each seaweed species and three additional replicate pieces of each seaweed (autogenic controls) were placed in cells without sea hares to measure changes in mass unrelated to consumption. Algae were assigned randomly to cells across treatments.

The red seaweeds used were *Amphiroa anceps* ((Lamarck) Decaisne, 1842), *Gracilaria halogenea* (Millar, 1990), *Galaxaura marginata* ((Ellis & Solander) Lamouroux, 1816), *Asparagopsis armata* (Harvey, 1855), *Nitophyllum delicatum* (Millar, 1990), *Laurencia rigida*, *Scinaia australis* ((Setchell) Huisman, 1985), *Solieria robusta* ((Greville) Kylin, 1932), *Hypnea johnstonii* (Setchell & Gardner, 1924) and the apical parts of bleached and healthy *D. pulchra*. *Delisea pulchra* at shallow depths (<5 m) becomes bleached on the apical parts of the thalli during spring/summer and may be less palatable to *A. parvula*. The green seaweeds used were *Caulerpa scapelliformis* ((R. Brown *ex* Turner) C. Agardh. Harvey, 1858) and *Ulva* sp. The brown seaweeds used were juvenile *Ecklonia radiata* (Hornemann, 1828), *Sargassum vestitum* ((R. Brown *ex* Turner) C. Agardh, 1820), *Sargassum linearifolium* ((Turner) C. Agardh, 1820), *Colpomenia sinuosa* ((Mertens *ex* Roth) Derbes and Solier, 1851), *Dictyota dichotoma* ((Hudson) Lamouroux. Harvey, 1847) and *Zonaria diesingiana* (J. Agardh, 1841).

Seaweeds were identified using existing keys (Womersley 1984, 1987; Farrant and King 1988; Millar 1990) and were collected on 12 November 1997 from Astrolabe Cove, Congwong Bay or Shark Bay. The pieces of seaweed used were 0.5 –1 g (wet wt) and sea hares were allowed to feed for 3 days, after which time each piece was reweighed. Pieces were taken from the upper parts of large seaweeds, whereas whole plants were used for smaller species. Consumption data are presented as g wet wt seaweed eaten per g wet wt *A. parvula* per day (g g^{-1} day^{-1}) so as to correct for differences in the size of sea hares. Before calculation of these values, data for each seaweed were corrected for autogenic changes by subtraction of the mean change in the mass of autogenic controls.

Statistical analyses

Abundance data for *Delisea pulchra*, *Laurencia obtusa* and *Aplysia parvula* at survey sites were highly heteroscedastic following appropriate transformations and Cochran's test, so no formal comparison was made between survey sites. To investigate whether there was a relationship between the abundance of *A. parvula* and that of *D. pulchra*, data from the Cruwee Cove and Congwong Bay survey sites (where both *A. parvula* and *D. pulchra* occurred) were pooled, then analysed by linear regression. To determine whether there was a relationship between the abundance of *A. parvula* and sea temperature, survey data for Cruwee Cove and Congwong Bay were pooled and analysed by linear regression.

Collections of *D. pulchra* from Astrolabe Cove (July 1995) were combined and analysed as one data set using linear regression to determine whether there was any relationship between the abundance of sea hares and the variables measured (abundance of other herbivores, algal physical characteristics or levels of secondary metabolites). The abundance of *A. parvula* on *D. pulchra* or *L. obtusa* in collections (no. g^{-1} algae) was also compared using Student's *t*-test. The frequency of activity of *A. parvula* on *D. pulchra* was analysed using a *G*-test with Williams's correction (Sokal and Rohlf 1995) to test the null hypothesis that activity is independent of diel sampling time. The mean consumption of different seaweeds by *A. parvula* was compared with zero by Student's *t*-test using Excel 4.0 (Microsoft Corp., Seattle, WA).

Results

Distribution of Aplysia parvula

Aplysia parvula was found on four species of algae during surveys at Congwong Bay, Cruwee Cove and Shark Bay. Of the 206 animals found during surveys, 82.5% occurred on *Delisea pulchra*, 13.1% occurred on *Laurencia obtusa*, 3.9% occurred on *Sargassum linearifolium*, and 0.5% occurred on *Dictyota dichotoma*. At other sites investigated on the NSW south coast, *A. parvula* was observed on several red algae, including *Asparagopsis armata*, *Plocamium cartilagineum*, *Solieria robusta* and an unidentified *Laurencia* sp. These red algae were uncommon or ephemeral in occurrence and non-coralline rhodophytes generally represented a small proportion of algal cover at survey sites (Fig. 1), except at Congwong Bay, where *Delisea pulchra* formed dense patches.

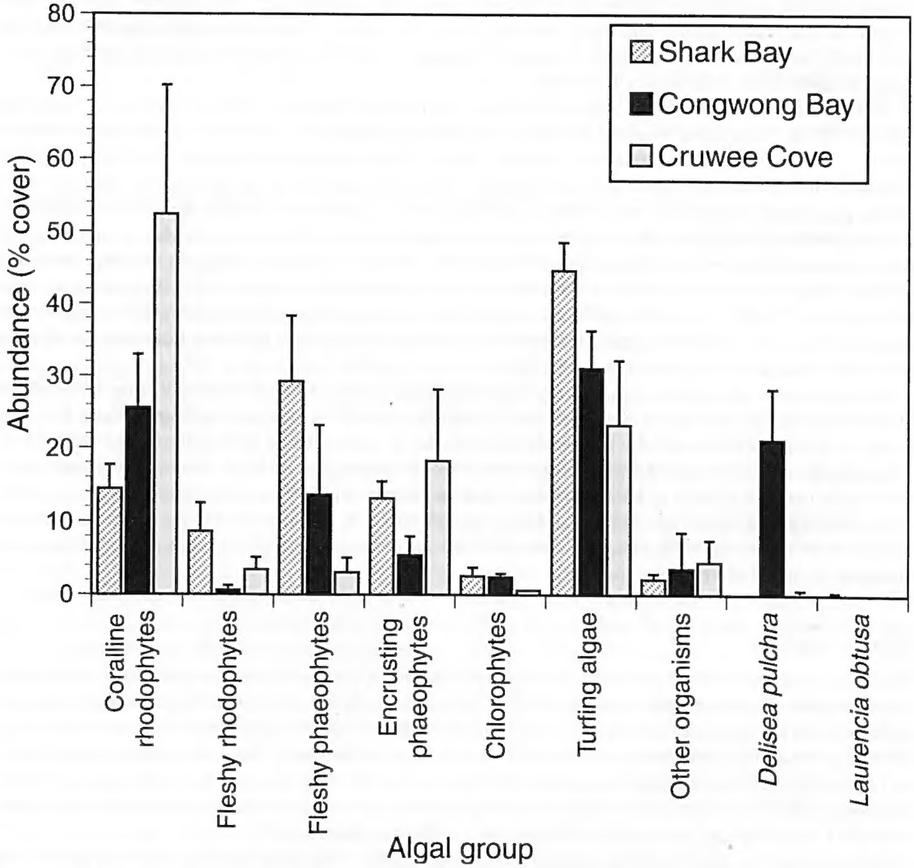

Fig. 1. Mean (± s.e.m.) abundance (percentage cover) of algal groups and the host algae (*Delisea pulchra* and *Laurencia obtusa*) of *Aplysia parvula* at field sites for all surveys.

Abundance of Aplysia parvula *and host algae*

Delisea pulchra occurred in high abundance at the Congwong Bay site (mean (± s.e.m.) 21.5 ± 7.0% cover), although this population declined in abundance over time (Fig. 2*a*). Coincident with the final phase of this decline was the mass recruitment of the sea urchin *Heliocidaris erythrogramma* (Valenciennes, 1846) onto the reef at Congwong Bay (see Wright and Steinberg 2001). The abundance of *Delisea pulchra* was consistently low at Cruwee Cove (0.4 ± 0.2% cover), as was that of *Laurencia obtusa* at Shark Bay (0.2 ± 0.1% cover; (Fig. 2*b,c*). *Laurencia obtusa* did not reach the high abundances observed prior to surveys at Shark Bay; it is seasonal in occurrence (Fig. 2*c*), but can form dense patches during the summer or autumn in Port Jackson. *Aplysia parvula* was found infrequently on the brown seaweed *Sargassum linearifolium*. Brown seaweeds (especially the genus *Sargassum*) were abundant at survey sites, except Cruwee Cove (Fig. 1). Coralline red algae also formed a substantial proportion of algal cover across survey sites and turfing algae (typically filamentous forms <3 cm) were also abundant at all sites (Fig. 1).

Aplysia parvula was most abundant at Congwong Bay (Fig. 2*a*), with generally lower abundance at Cruwee Cove and Shark Bay (Fig. 2*b,c*), although the highest abundance of

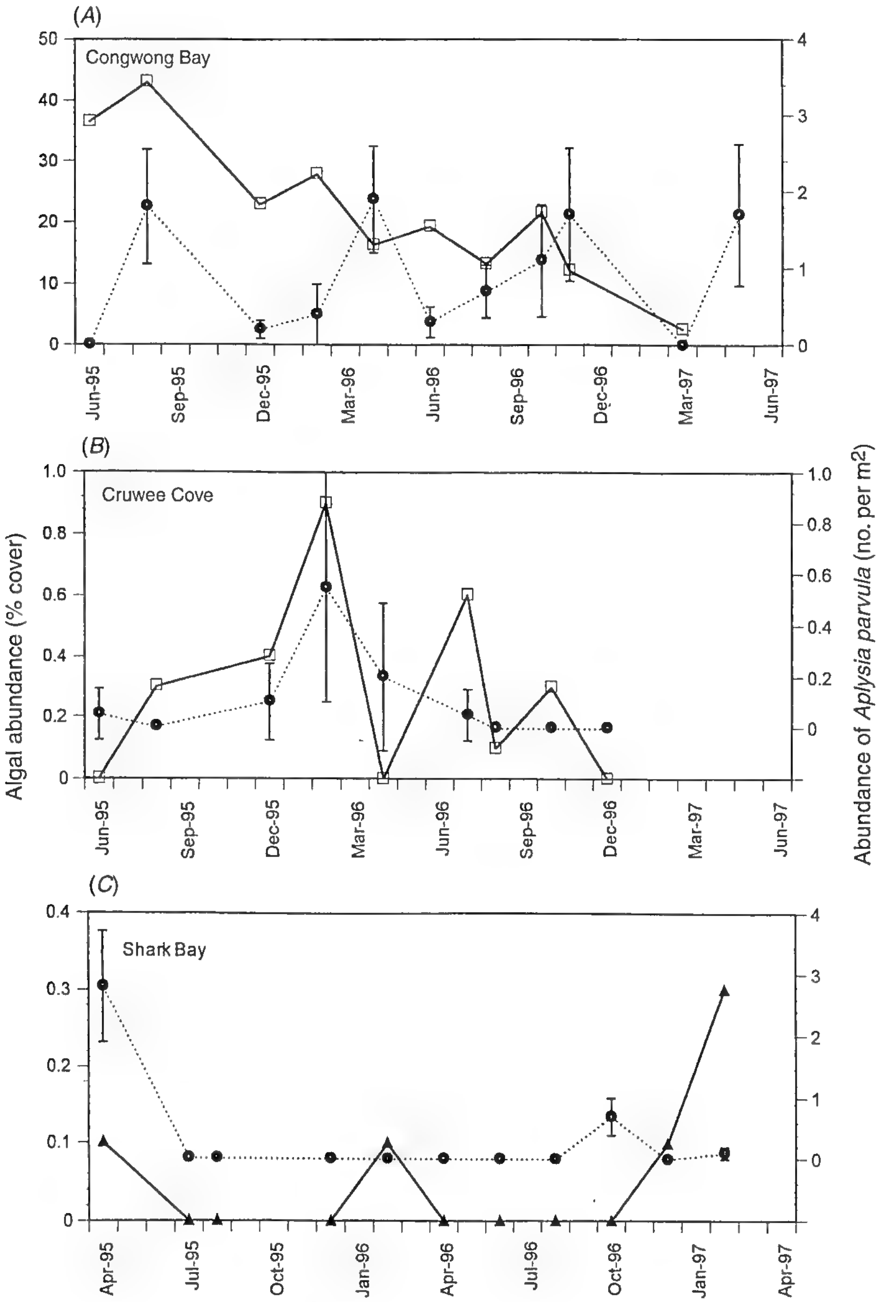

Fig. 2. Abundance of *Aplysia parvula* and host algae at fixed sites during temporal surveys. The mean (± s.e.m.) abundance of *A. parvula* (●) is shown for each survey. *A*, Congwong Bay surveys, including the mean abundance of *Delisea pulchra* (□). *B*, Cruwee Cove surveys, including the mean abundance of *D. pulchra* (□). *C*, Shark Bay surveys, including the mean abundance of *Laurencia obtusa* (▲). Error bars for algal abundance were omitted to emphasise variation in sea hare abundance.

A. parvula recorded during surveys was 2.80 ± 0.92 sea hares per m^2 on *L. obtusa* at Shark Bay. *Aplysia parvula* was present year round on *D. pulchra* and was present during the summer and autumn on *L. obtusa* (Fig. 2). *Aplysia parvula* inhabiting *D. pulchra* at Congwong Bay appeared to show regular peaks in abundance separated by intervals of 6–8 months (Fig. 2*a*) that were of similar magnitude, despite the declining abundance of *D. pulchra*. There was a significant relationship between the abundance of *A. parvula* and percentage cover of *D. pulchra* ($y = 0.25x + 0.06$; $r^2 = 0.32$; $P = 0.01$; $n = 18$) for pooled data (Cruwee Cove and Congwong Bay). The low abundance of *L. obtusa* at the Shark Bay site precluded an analysis of the relationship between the abundance of *A. parvula* and this seaweed. The abundance of *A. parvula* on *D. pulchra* (pooled data) showed no relationship to sea temperature when examined using linear regression ($y = -0.03x + 1.41$; $r^2 = 0.01$; $P = 0.720$, $n = 18$). Overall, *D. pulchra* occurred in greater abundance than *L. obtusa* in both space and time, and *D. pulchra* was the major host plant for *A. parvula* near Sydney.

Factors associated with variation in the abundance of Aplysia parvula

Delisea pulchra was collected to investigate biotic, physical and chemical factors that may influence the abundance of *Aplysia parvula* on this seaweed. There were significant relationships between the abundance of *A. parvula* and several of the variables measured (Table 1). The only positive relationship found was between the abundance of *A. parvula* and that of the herbivorous 'prosobranch' gastropods recorded (see Materials and methods). Other significant linear regressions had negative slopes, including plant weight and the concentrations of the secondary metabolites (furanone 1, furanone 2 and total furanones). There was no significant relationship between sea hare abundance and the physical characteristics of plant conical volume or density. These results suggest that *A. parvula* prefer to inhabit smaller plants with lower levels of metabolites. However, the r^2 statistics for these regression analyses are low (Table 1), which diminishes their biological significance. Collections of algae showed a different pattern of abundance of sea hares compared with surveys. *Aplysia parvula* was significantly more abundant on individual *Laurencia obtusa* plants (mean 0.214 ± 0.027 sea hares g^{-1} algae wet wt; $n = 28$ plants) than on *Delisea pulchra* (0.068 ± 0.028 sea hares g^{-1} algae wet wt; $n = 15$ plants) when compared

Table 1. Factors affecting the abundance of *Aplysia parvula* on *Delisea pulchra*

Regression analyses of the abundance of *A. parvula* (no. sea hares per g wet weight (wt) algae) compared with the abundance of co-occurring herbivores (no. herbivores per g wet wt algae) or the physical and chemical properties of *D. pulchra* collected from Astrolabe Cove in July 1995. The regression equations are of the form $y = ax + b$ where y is the abundance of *A. parvula* and x is the listed variable. Significant results are indicated by asterisks ($n = 58$)

Variable	*a*	*b*	r^2	*P*
Abundance of 'prosobranch' gastropods	0.336	–0.016	0.22	<0.001*
Abundance of *Holopneustes purpurescens*	–0.450	0.017	0.02	0.419
Plant length (cm)	–0.002	0.045	0.01	0.406
Plant conical volume (cm^3)	<0.001	0.036	0.04	0.144
Plant weight (g wet wt)	–0.001	0.063	0.12	0.009*
Plant density ($g\ cm^{-3}$)	0.143	0.011	<0.01	0.896
Furanone 1 concentration ($mg\ g^{-1}$ dry wt)	–0.106	0.055	0.09	0.022*
Furanone 2 concentration ($mg\ g^{-1}$ dry wt)	–0.071	0.041	0.08	0.038*
Furanone 3 concentration ($mg\ g^{-1}$ dry wt)	–0.060	0.032	0.06	0.078
Furanone 4 concentration ($mg\ g^{-1}$ dry wt)	–0.066	0.038	0.06	0.056
Total furanone concentration ($mg\ g^{-1}$ dry wt)	–0.021	0.045	0.08	0.029*

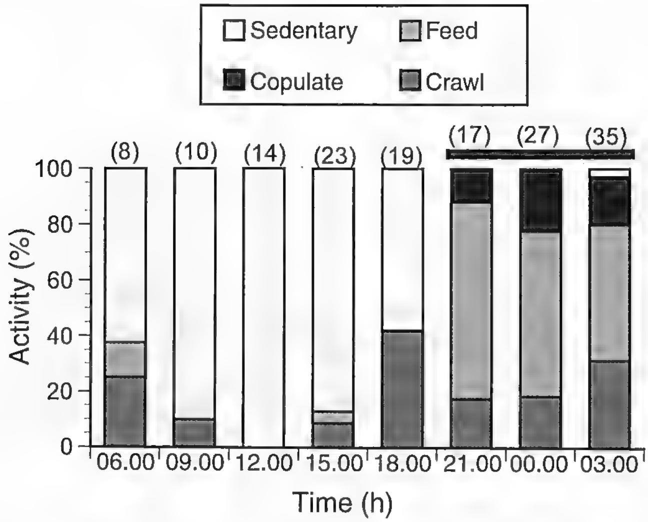

Fig. 3. Diel activity patterns of *Aplysia parvula* on *Delisea pulchra* at Congwong Bay. Histograms show the percentage of individuals engaged in each activity. The line above the bars indicates night sampling. The number of sea hares per sample (n) is given above each bar in parentheses.

using two-tailed Student's t-test ($t = -3.53$; $P = 0.001$). This difference may be attributable to the concentration of sea hares on *L. obtusa*, because this alga occurred at low abundances in Port Jackson.

Activity patterns

Aplysia parvula was nocturnal, with most sea hares grazing or copulating at night (Fig. 3). The activity of *A. parvula* on *Delisea pulchra* was not independent of diel sampling time ($G_{adj} = 151.25$, $\chi^2_{0.001[21]} = 46.80$; $P << 0.001$), suggesting that the activity of this sea hare varies significantly during the diel cycle. The population surveyed consisted of both adult and juvenile sea hares (<1 cm in length) and all showed similar patterns of activity. *Aplysia parvula* became active during the afternoon, moving up the thalli of *D. pulchra*. After dusk, most emerged onto the canopy of *D. pulchra* and began to feed, whereas some copulated. Feeding was the most frequently recorded activity at night, although there was no apparent pattern in which activities occurred over time, with sea hares moving, feeding and mating throughout the night. Sea hares moved back down the thalli of *D. pulchra* before dawn and most remained sedentary until the following afternoon. A few *A. parvula* individuals were observed feeding on basal parts of *D. pulchra* during the day (Fig. 3). No egg laying was observed at night and egg masses were found most often in the mid to basal parts of *D. pulchra* thalli, suggesting that egg laying may occur during the day. *Aplysia parvula* had a similar pattern of nocturnal activity on *Laurencia obtusa* in Port Jackson (C. N. Rogers, unpublished observation).

Dietary range of Aplysia parvula

Aplysia parvula consumed a variety of co-occurring red, green and brown algae. However, red algae were consumed most often and in greater quantities than either green or brown

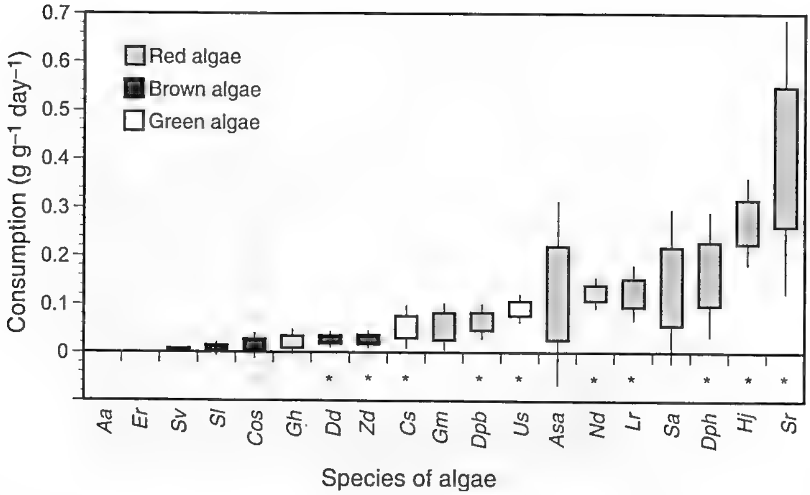

Fig. 4. Dietary range of *Aplysia parvula*. Data are the mean ± s.e.m. consumption (bars), measured as g algae eaten (wet weight) per g sea hare (wet weight) per day, and 95% confidence limits (lines). Consumption data were corrected for autogenic changes in algal mass. Mean consumption of each alga was compared with zero by Student's *t*-test. Consumption that is significantly different from zero at $P = 0.05$ is indicated (asterisk); $n = 5$ (except *Galaxaura marginata* (*Gm*) and *Zonaria diesingiana* (*Zd*), where $n = 4$). *Aa*, *Amphiroa anceps*; *Er*, juvenile *Ecklonia radiata*; *Sv*, *Sargassum vestitum*; *Sl*, *Sargassum linearifolium*; *Cos*, *Colpomenia sinuosa*; *Gh*, *Gracilaria halogenea*; *Dd*, *Dictyota dichotoma*; *Cs*, *Caulerpa scapelliformis*; *Dpb*, bleached *Delisea pulchra*; *Us*, *Ulva* sp.; *Asa*, *Asparagopsis armata*; *Nd*, *Nitophyllum delicatum*; *Lr*, *Laurencia rigida*; *Sa*, *Scinaia australis*; *Dph*, healthy *D. pulchra*; *Hj*, *Hypnea johnstonii*; *Sr*, *Solieria robusta*. Algal divisions are indicated by the different shading of bars.

algae (Fig. 4). The alga *Solieria robusta* was highly consumed by *A. parvula* (at a mean rate of 0.405 ± 0.144 g g^{-1} day^{-1} after correction for autogenic changes). Several red algae were consumed at equivalent or higher levels than healthy *Delisea pulchra*, the host alga from which the sea hares were collected (Fig. 4). Bleached pieces of *D. pulchra* were consumed less by sea hares (0.064 ± 0.018 g g^{-1} day^{-1}) than healthy pieces (0.161 ± 0.066 g g^{-1} day^{-1}), suggesting that such damage lowers the palatability of the algal tissues. Consumption was significantly different from zero for eight non-host algae including red algae of the Ceramiales and Gigartinales, green algae of the Caulerpales and Ulvales, and Dicyotalean brown algae (Fig. 4). This indicates that *A. parvula* has generalised feeding habits, especially on red algae, which contrasts with their restricted distribution on host algae in the field. The brown alga *Sargassum linearifolium* was not eaten, although *A. parvula* was occasionally found on this seaweed during surveys. Consumption of the calcified red algae *Galaxaura marginata* and *Amphiroa anceps* was not significantly different from zero, yet some *A. parvula* individuals consumed the lightly calcified *G. marginata*.

Discussion

Distribution and abundance of Aplysia parvula *and host algae*

Aplysia parvula was found primarily on red seaweeds from three different orders (Bonnemaisoniales, Ceramiales and Gigartinales), similar to host ranges reported

previously for this sea hare (Willan 1979; Switzer-Dunlap and Hadfield 1981; Carefoot 1987, 1989). *Aplysia parvula* also occurred at very low densities on the brown algae *Sargassum linearifolium* and *Dictyota dichotoma*. Many of the red seaweeds investigated here were uncommon and/or seasonal and habitation of such seaweeds (e.g. *Laurencia* spp., *Asparagopsis armata*) by *Aplysia parvula* suggests that this sea hare is highly opportunistic, using any suitable algae. For *A. parvula*, host plant choice appears restricted to chemically rich red seaweeds that may allow this sea hare to evade and/or deter predatory fish (Ginsburg and Paul 2001; Rogers *et al.* 2002). The processes affecting the distribution of *A. parvula* (e.g. selective larval settlement, post-settlement mortality) were not tested in the present study.

Aplysia parvula was most abundant on two red algae, namely *Delisea pulchra* and *Laurencia obtusa*, near Sydney. These algae differ in occurrence; *D. pulchra* was present year round and formed large beds at some sites. *Delisea pulchra* has been reported to be one of the most abundant red seaweeds on the NSW coast (Millar 1990) and, thus, provides *A. parvula* with access to a large, persistent resource. The abundance of *A. parvula* was significantly related to the abundance of *D. pulchra*. In contrast, *L. obtusa* was found mainly in Port Jackson, where it occurred occasionally in dense patches. The relationship between the abundance of *L. obtusa* and that of *A. parvula* could not be adequately addressed from the Shark Bay survey data, because *L. obtusa* did not occur at the high abundances observed previously. However, the abundance of *A. parvula* on *L. obtusa* was measured in collections from other parts of Port Jackson and sea hares were threefold more abundant per gram *L. obtusa* compared with *D. pulchra*. *Laurencia obtusa* has been reported to be widespread in temperate and tropical waters (Millar 1990) and may provide a major resource for *A. parvula* at other localities.

Aplysia parvula occurred year round on *D. pulchra*, although its abundance on this seaweed fluctuated. Pennings (1991*a*) found *A. californica* to be present year round and attributed changes in its abundance to variation in recruitment. Fluctuations in the abundance of *A. parvula* may also be due to variable recruitment, although this was not measured in the present study. Another possibility is predation pressure on *A. parvula*, because some reef fish are now known to consume sea hares (Ginsburg and Paul 2001; Pennings *et al.* 2001; Rogers *et al.* 2002) and fish were observed to feed from *D. pulchra* both during the day and at night (C. N. Rogers, unpublished observations). Such continuous predation pressure may rapidly reduce sea hare populations during and after recruitment events. Although the age structure of *A. parvula* was not examined, the variable pattern of abundance suggests that *A. parvula* may persist for only a few months on *D. pulchra*.

The abundance of *A. parvula* on *D. pulchra* was weakly associated with several factors. Abundance was negatively related to the weight (size) of *D. pulchra*. One possible explanation for this pattern is that smaller plants are younger and have more palatable tissues, which are preferred by herbivores (e.g. Cronin and Hay 1996). The positive relationship between the abundance of *A. parvula* and the abundance of other herbivorous gastropods (i.e. *Phasioanotrochus eximius* and *Dentimitrella lincolnensis*) may also indicate that smaller *D. pulchra* individuals are, in general, higher preference foods for mesograzers. The negative relationships between the abundance of *A. parvula* and concentration of secondary metabolites (furanones 1 and 2 and total furanones) may indicate that this sea hare prefers to inhabit algae with lower concentrations of these compounds. This result further supports the notion that consuming *Delisea pulchra* has a fitness cost for *A. parvula* (Rogers *et al.* 2002). No other study has attempted to relate sea hare abundance on host plants to their physical and chemical properties, so it is unknown

how general these results are. The red algae inhabited by *A. parvula* typically have complex habits, with densely packed thalli. However, *A. parvula* showed no preference for high thalli density among *D. pulchra* individuals. Other marine herbivores, including amphipods (Hacker and Steneck 1990) and crabs (Kennish and Williams 1997), show strong preference for seaweeds with particular morphologies. Suggested reasons for such selectivity include refuge value, attachment ability and restricted feeding structures (Hacker and Steneck 1990; Kennish and Williams 1997).

Activity patterns

Aplysia parvula was mostly active at night on *Delisea pulchra* and *Laurencia obtusa* near Sydney, moving, grazing and copulating in the canopy of these algae. In contrast, *A. parvula* in Hawaii is active over the entire diel cycle, with grazing occurring mostly in the afternoon (Carefoot 1989). Furthermore, Hawaiian *A. parvula* occupies cryptic positions at the base of algae at night rather than during the day (Carefoot 1989). The sea hare *A. dactylomela* exhibits the same nocturnal activity patterns in Hawaii (Carefoot 1989) and Jamaica (Carefoot 1991), and *A. dactylomela* in Port Jackson was also observed to be nocturnal, although large adults change their habits and forage or copulate during the day. The factors affecting activity patterns in sea hares appear to vary with ontogeny (at least for *A. dactylomela*) and geographic location and may warrant further research.

Diet and feeding by Aplysia parvula

Aplysia parvula consumed a variety of red, green and brown algae. This generalised feeding pattern is similar to that found for other sea hares (Carefoot 1987). However, this contrasts with the restricted distribution of *A. parvula* on *Delisea pulchra* and *Laurencia obtusa* that was found during field surveys. *Solieria robusta* (which lacks known secondary metabolites) was eaten at the highest rate by *A. parvula*, but is uncommon and grows in deeper habitats than those in which *A. parvula* is typically found. The sparsely branched habit of *S. robusta* may provide less shelter from predators for sea hares compared with other host algae. Interestingly, several red seaweeds were consumed at higher rates than the dominant host *D. pulchra* from which the *A. parvula* individuals were collected. The host alga *L. obtusa* (not tested here) was consumed at the greatest rate by *A. parvula* in the study of Rogers (1999), with a mean (± s.e.m.) feeding rate of 0.884 ± 0.043 g g^{-1} day^{-1}, some fivefold greater than for *D. pulchra*. *Aplysia parvula* preferentially consumed the apical tissues and lateral buds of both *D. pulchra* and *L. obtusa* (Rogers 1999). Such preferences for softer or younger tissues have been reported previously in sea hares (Carefoot 1987; Pennings 1990*a*) and other marine herbivores (Poore 1994; Cronin and Hay 1996). *Aplysia dactylomela* and *A. sydneyensis* (Sowerby, 1869) also consume *L. obtusa* and inhabit it as juveniles (C. N. Rogers, unpublished observation). Juveniles of these species may compete with *A. parvula* for *L. obtusa*, as suggested by Willan (1979). *Aplysia parvula* has more exclusive use of *D. pulchra* because only a few individual *A. juliana* and *A. sydneyensis* were found on this alga during surveys.

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First report of the European flat oyster *Ostrea edulis*, identified genetically, from Oyster Harbour, Albany, south-western Western Australia

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Abstract

Ostrea angasi is the only large native ostreine species in southern Australian waters (i.e. New South Wales, Victoria, Tasmania, South Australia and Western Australia (WA)). It has also been recorded as a fossil from Late Pliocene calcarenites of the Roe Plain along the south-eastern coast of WA. Wild populations were harvested for food before and after European settlement. A sample of flat oysters from Oyster Harbour, Albany, WA, was typed for *16S* and cytochrome oxidase 1 (*CO1*) mitochondrial (mt) DNA markers previously shown to be diagnostic for species of Ostreidae. *Ostrea edulis* was identified in the sample at an approximate 30% occurrence with *O. angasi*. Interspecific partial *16S* and *CO1* mtDNA sequence divergences, estimated using Kimura's two-parameter model, were 0.83% and 1.45%, respectively. The occurrence of *O. edulis* among native *O. angasi* populations has not hitherto been suspected and, thus, there has not been a legitimate morphological separation of the two. These results emphasise the value of molecular markers in: (*1*) discriminating morphologically plastic and closely related species; and, thus (*2*) the monitoring of species introduced into morphologically similar stocks. We caution against such introductions because of the possibility of the importation of oyster diseases (e.g. bonamiasis) and of this and other adverse impacts upon native species.

Additional keywords: Bonamia, cytochrome oxidase 1 (*CO1*) gene, *16S* gene, introduced species, *Ostrea angasi*.

Introduction

Wild populations of native flat oysters were harvested for food in many parts of southern Australia before and after European settlement. Dakin (1952) noted that: '…to judge by the remains found in their coastal kitchen-middens the aborigines evidently appreciated it, and it must at one time have been relatively common even around Sydney'.

The identity of the southern Australian flat oyster has been debated for many years. Tenison-Woods (1877–1878) considered that both *Ostrea edulis* (Linnaeus, 1758) and *Ostrea angasi* (Sowerby, 1871) occurred in Tasmania. Saville-Kent (1895) considered that the so-called mud-oyster abundant in the vicinity of Albany, Western Australia (WA), was *O. edulis* being '…identical with the British 'Native''. The common flat oyster of South Australia (SA) and New South Wales (NSW) was considered by Allan (1950) to be *Ostrea sinuata* (Lamarck, 1819), although this author also noted that, in 1947 and 1948, '…seeds of the large Japanese edible oyster, *Ostrea gigas*, were transported from Japan to beds in Tasmania and Western Australia'. This suggests that, at least prior to this date, it was common for oysters to be introduced from elsewhere without significant hindrance and this may have some relevance to the present study. Cotton and Godfrey (1938), Dakin (1952) and Cotton (1961) also considered that *O. sinuata* was the common flat oyster of SA.

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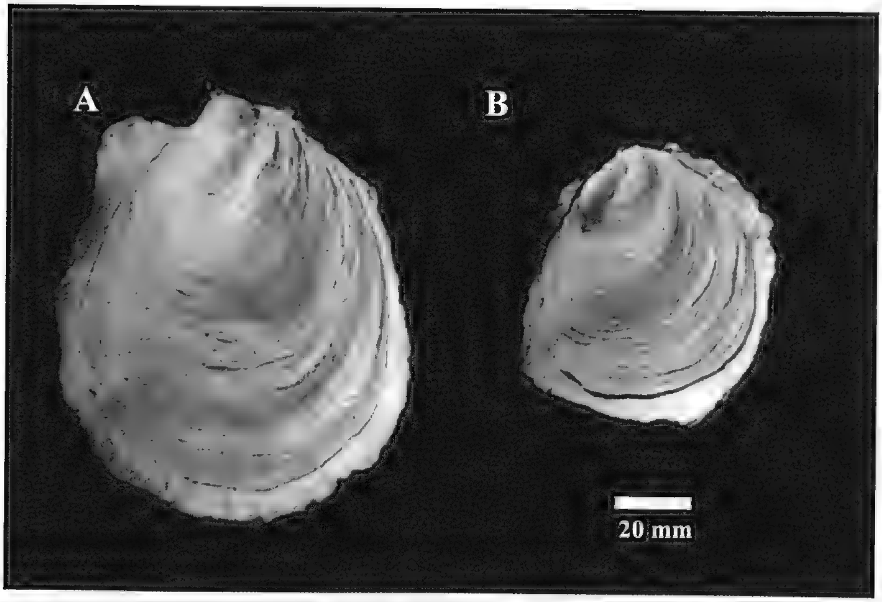

Fig. 1. Native fossil flat oysters in Western Australia (WA) are *Ostrea angasi. A*, Fossil *O. angasi* from an emergent Middle Holocene shell bed at Cervantes, near the coast, northern Perth Basin, Western Australia; *B*, fossil *O. angasi* from the Late (though not latest) Pliocene of the Roe Calcarenite of the Eucla Basin, WA. See Fig. 2 for collection sites. These specimens are from the collections of the Western Australian Museum with reference numbers WAM 82.2891.b and WAM 69.536.a, respectively.

However, Thomson (1954) considered that the correct name for the native Australian oyster was *Ostrea angasi*, with *O. sinuata* as a junior synonym, and Ludbrook and Gowlett-Holmes (1989) also describe *O. angasi* as the only flat oyster present in southern Australia. Edgar (1997) considers that *O. angasi* occurs from Fremantle, WA, to NSW and around Tasmania and is '...virtually indistinguishable from the European oyster *Ostrea edulis*'. Roberts and Wells (1981) also give the same distribution for *O. angasi*, whereas Lamprell and Healy (1998) are the most recent authors to consider that *O. sinuata* (Cotton and Godfrey, 1938, non-Lamarck, 1819) is a junior synonym of *O. angasi* and also give it a wide, southern distribution in WA, SA, Tasmania, Victoria and NSW. Jozefowicz and O' Foighil (1998) sequenced the *16S* gene of eight flat oyster individuals from St Helens, Tasmania, and Pambula, NSW, and all were genetically identified as *O. angasi*.

Thus, *O. angasi* is considered to be the only large ostreine species in southern Australian waters. It has also been recorded as a fossil from the mid-Holocene of Cervantes, north of Perth, and the Late Pliocene calcaranites of the Roe Plain along the southern coast of WA (Slack-Smith 2000; Fig. 1).

In (Albany) WA, in 1791, Vancouver records that he:

> '...found a passage, narrow and shoal for some distance, into the north-eastern harbour; where a bar was found to extend across its entrance, on which there was only three fathoms [6 m] of water...In our way out of this harbour, the boats grounded on a bank we had not before perceived; this was covered with oysters of a most delicious flavour, on which we sumptuously regaled; and, loading in about half an hour, the boats for our friends on board, we commemorated the discovery by calling it Oyster Harbour' (Vancouver 1798).

Twelve years later, in 1803, Baudin prepared to go and visit the head of the port (Oyster Harbour) and reconnoitre the oyster-beds spoken of by Vancouver:

> 'We finally reached the head of the port and stood off the edge of a shoal, where we collected a reasonable number of oysters 1½ to 2 feet down on a bed of weeds [actually seagrasses]. They were found to have a good flavour and to be extremely big' (Baudin 1809).

As with the flat oysters in all of southern Australia, in WA the species attracted attention as a fisheries object from the earliest days and its name thereat followed the fortunes of its conspecifics in other parts of the country.

Saville-Kent (1894) considered '...*Ostrea edulis*...is common to the colonies of Victoria, Tasmania and South Australia' and '...was abundant in the vicinity of Albany'. Saville-Kent (1895) reiterated the above, but pointed out that the oyster had been '...so exhaustively fished as to have been almost exterminated' and that '...steps are now being taken by Government...to re-establish the oyster beds of King's Sound [i.e. King George Sound]'. The same proposals were reiterated in 1897 and 1898 (Anonymous 1897, 1898) but, thereafter, it seems no identified action was taken and the industry in Albany was allowed to die, the market for local oysters being taken up by crassostreine rock oysters of the genus *Saccostrea* being sent down to Perth and Fremantle from the neighbourhoods of Shark Bay and Geraldton with '...supplementary importation from Queensland and New South Wales' (Anonymous 1999).

With the decline of *O. angasi* in Oyster Harbour, Albany, rock oysters (*Saccostrea glomerata*) introduced from more western coasts of WA are farmed there today (Anonymous 1999). The numbers of wild individuals of *O. angasi* in Oyster Harbour are still now so low that this species is no longer a significant fisheries product. However, in 2002, samples of flat oysters living in Oyster Harbour were obtained and their identities studied using mitochondrial (mt) DNA sequences and shell characteristics.

Materials and methods

In 2002, samples of flat oysters from Oyster Harbour, Albany, WA (Fig. 2), were typed for the *16S* and cytochrome oxidase 1 (*CO1*) mtDNA markers previously shown to be diagnostic for the Ostreidae (Jozefowicz and O'Foighil 1998). Genomic DNA was extracted from 10 individual oysters using Dneasy™ Tissue Kit (Qiagen, Venlo, the Netherlands). The partial *16S* and *CO1* segments were amplified using primer pairs of 16sar/16sbr (Banks *et al.* 1993) and LCO1490/HCO2198 (Folmer *et al.* 1994), respectively. Polymerase chain reaction (PCR) conditions followed those of Jozefowicz and O'Foighil (1998) and Lam *et al.* (2003). The PCR products were purified using Sephaglas™ BandPrep Kit (Amersham Pharmacia Biotech, Buckinghamshire, England) and then sequenced using an ABI Prism™ dRhodamine Terminator Cycle Sequencing Ready Reaction Kit (Buckinghamshire, England) and an ABI 377 Perkin Elmer (Buckinghamshire, England) DNA sequencer. The PCR primers were used as sequencing primers. Sequences of Albany individuals and other ostreines from GenBank (http://www.ncbi.nlm. nih.gov/, accessed May 2002) were aligned using ClustalX 1.81 (Thompson *et al.* 1997). Phylogenetic analysis and sequence divergence values were obtained using PAUP* 4.0b8 (Swofford 1998).

Comparisons were made between the shell characteristics of genetically identified individuals to clarify conchological distinctions. Shell characters involved were: (*1*) shape and surface sculpture; (*2*) external and internal shell colour; (*3*) hinge line and ligament position and extent; (*4*) attachment area of the left valve; (*5*) presence and pattern of chomata; and (*6*) position, colour and relative size of the adductor muscle scar.

Voucher specimens have been lodged in the Western Australian Museum, Perth (S10871 to S10874).

Results

Partial *16S* (approximately 445 nucleotides (nt)) and *CO1* (approximately 700 nt) sequences of 10 individuals (identified as Albany 1–10) and two individuals (Albany 1 and

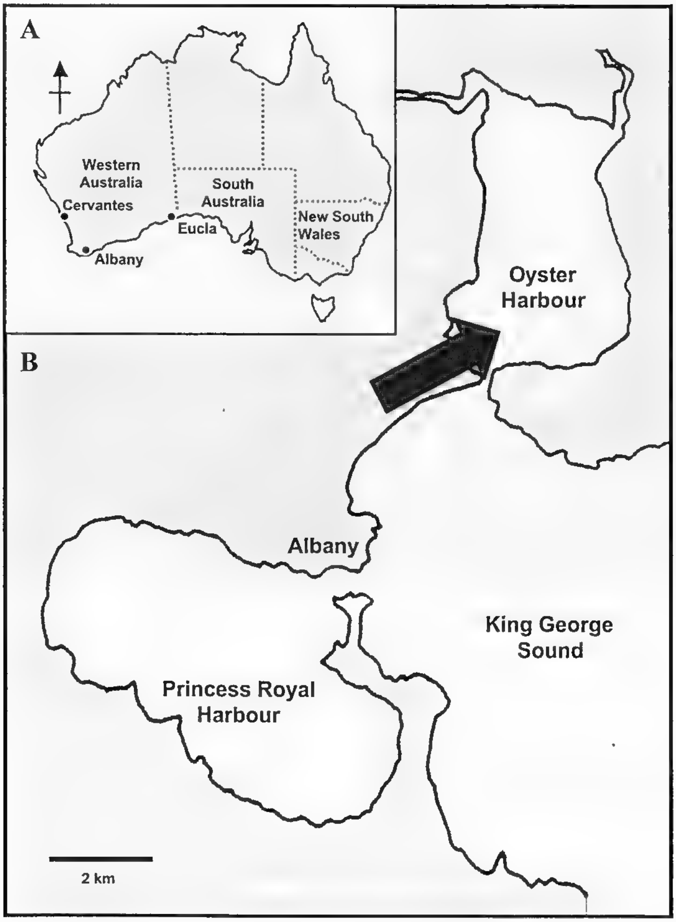

Fig. 2. *A*, Map of Australia showing the locations of the fossil *Ostrea angasi*. *B*, Detailed map of Albany, Western Australia, showing the collection site (arrow) for flat oysters.

Albany 2), respectively, of Albany flat oysters, locally identified as *O. angasi*, were obtained. Four and two haplotypes were obtained from the *16S* and *CO1* datasets, respectively. When these sequences of Albany flat oysters were compared with those published on GenBank using a BLAST network service, two taxa were identified. One was similar to *O. angasi* (for *16S*, GenBank accession number = AF052063 (Jozefowicz and O'Foighil 1998); for *CO1*, GenBank accession number = AF112287 (O'Foighil *et al.* 1999)) and the other was similar to *O. edulis* (for *16S*, GenBank accession number = AF052068 (Jozefowicz and O'Foighil 1998); for *CO1*, GenBank accession number = AF120651 (Giribet and Wheeler 2002)). For *16S*, one of the haplotypes is similar to the sequence of *O. angasi* from GenBank with one transition. The other three are similar to the sequence of *O. edulis* from GenBank with ranges from zero to one transition. The sequences reported upon herein have been deposited in GenBank under accession numbers AF540594–AF540599.

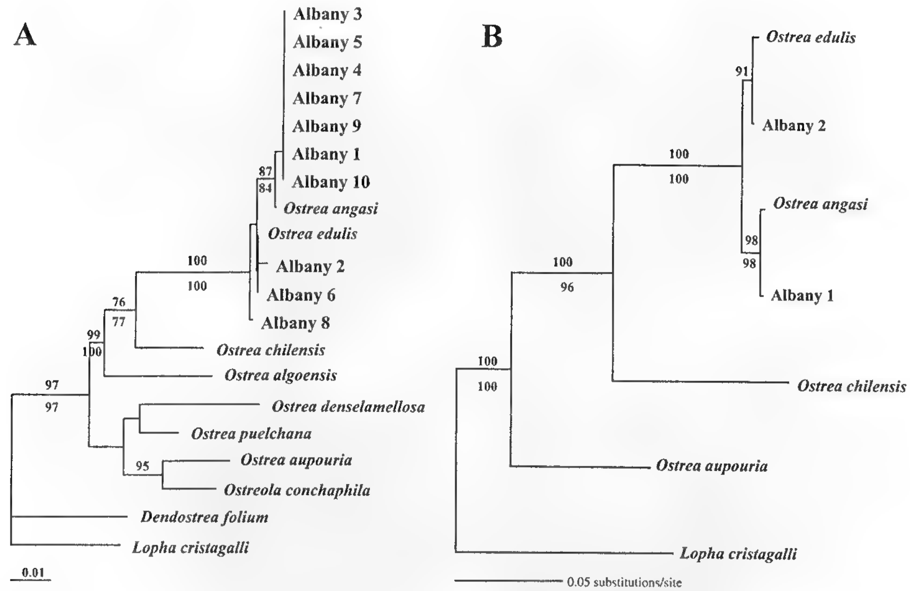

Fig. 3. *A*, Neighbour-joining (NJ) tree constructed using sequence divergence values based on the Kimura two-parameter model obtained from mitochondrial (mt) *16S* gene fragment (approximately 445 nucleotide) sequences for flat oysters of the Ostreinae. Members of the Lophinae were used as outgroups. Albany 1–10 represent ten individuals from Albany, Western Australia. Other oyster sequences were derived from Jozefowicz and O'Foighil (1998) (GenBank accession numbers AF052062–AF052069, AF052071 and AF052073). The tree topology of the 24 most parsimonious (MP) trees (131 steps; consistency index (CI) = 0.756; retention index (RI) = 0.822), obtained by heuristic search from the same dataset, is similar to that of the NJ tree. Bootstrap values (number of replicates = 1000) for NJ and MP trees are indicated above and below the branches, respectively. Only values >75 are shown. The scales represent the percentage of substitution. *B*, An NJ tree calculated using sequence divergence values based on the Kimura two-parameter model obtained from mt cytochrome oxidase I gene fragment (approximately 700 nucleotide) sequences for flat oysters of the Ostreinae. Albany 1 and Albany 2 represent two individuals from Albany. *Lopha cristagalli* was used as an outgroup (Matsumoto 2001; direct GenBank submission, GenBank accession number AB076908). Sequences of *O. chilensis*, *O. angasi*, and *O. aupouria* were derived from O'Foighil *et al.* (1999) (GenBank accession numbers AF112285, AF112287 and AF112288, respectively). The tree topology of the MP tree (248 steps; CI = 0.891, RI = 0.738), obtained by an heuristic search, is the same as that of the NJ tree.

The identities of *O. angasi* and *O. edulis* in Albany were confirmed further by molecular phylogenetic analysis of the two taxa and comparison with conspecifics from elsewhere and with other ostreine species (Fig. 3). Flat oysters, named Albany 1, 3, 4, 5, 7, 9 and 10, were identified genetically as *O. angasi*, whereas those named Albany 2, 6 and 8 were identified as *O. edulis*. Mean interspecific partial *16S* and *CO1* mtDNA sequence divergences, estimated using Kimura's two-parameter model, were 0.83% and 1.45%, respectively. Figures 4 and 5 show external and internal views of the valves of flat oysters from Albany that have been identified genetically as *O. angasi* and *O. edulis*.

Ostrea angasi shells are approximately 50 mm in dorsoventral height, subtriangular to oval in shape and slightly prosogyrous. Individuals are unattached and reside on the left valve. Shells are heavily bored by polychaetes and encrusted with balanoid barnacles. The right valve is nearly flat and heavily eroded dorsally, such that the chalky calcareous shell

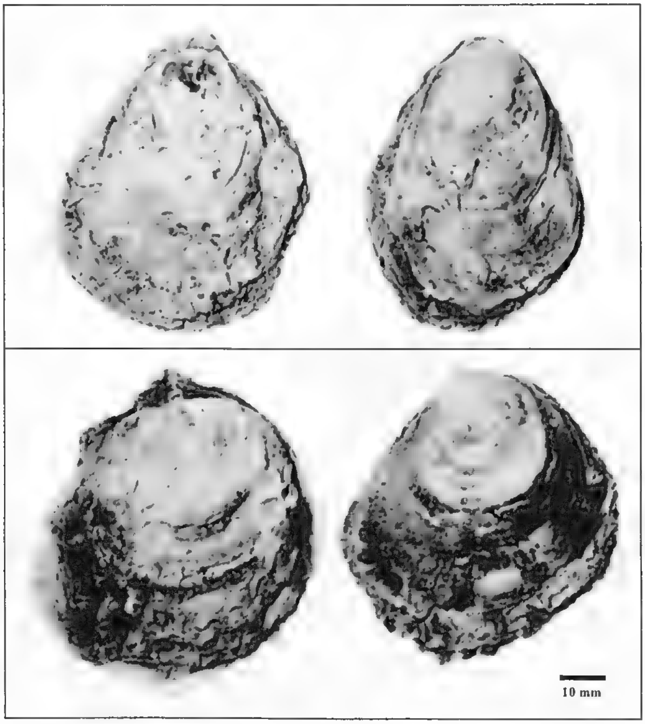

Fig. 4. Genetically identified shells of *Ostrea angasi* (top row) and *Ostrea edulis* (bottom row) collected from Oyster Harbour, Albany, Western Australia. External surfaces of the right valves are shown.

layer is exposed. The ventral margin is covered by dense layers of brown, overlapping, thin and brittle lamellae or scales arising from growth lines. The left valve is more inflated than the right and white. Chomata are absent. The hinge line is straight and short. The ligament area is slightly extended in both valves. The interior of the shell has white and bluish–green patches with a pearly nacre. Small patches of chalky deposits are prominent on the interiors of both the left and right valves. The adductor muscle scar is white with lightly coloured growth lines. It is anteroposteriorly elongate, crescentic and positioned in the posterior ventral one-third of the pallial area.

Ostrea edulis shells are also approximately 50 mm in dorsoventral height, but have a subcircular outline and are distinctively opisthogyrous. Because the right valve is less eroded, fouled and bored, layers of brown growth lamellae with dark radial rays are obvious. The layer of lamellae in *O. edulis* is less dense than that in *O. angasi*. The left valve is more inflated than the right and is white with low, widely spaced radial ribs. Individuals are unattached and, like *O. angasi*, also reside on the left valve. Chomata are absent. The hinge line is straight and short and the ligament area is slightly extended in both valves. The interior of the shell is white with lightly coloured patches on the ventral side. Large patches of chalky deposits are prominent on the interiors of both left and right valves. The adductor muscle scar is white with lightly coloured growth lines. This scar is anteroposteriorly elongate, crescentic and tapers posteriorly. It is centrally positioned, slightly near the posterior.

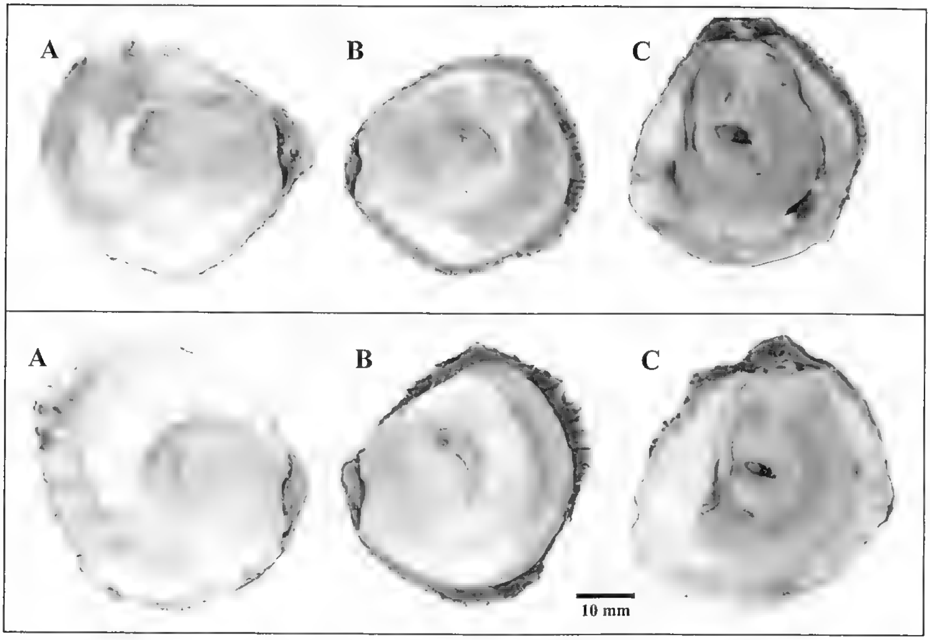

Fig. 5. Genetically identified shells of *Ostrea angasi* (top row; WAM S10872) and *Ostrea edulis* (bottom row; WAM S10874) collected from Oyster Harbour, Albany, Western Australia. *A*, Internal views of the right valves; *B*, internal views of the left valves; *C*, internal views of the left valves showing the organs of the mantle cavity.

Anatomical structures, such as the shape and position of the adductor muscle and the arrangement, relative size and colour of various organs in the mantle cavity are similar in the two species. Therefore, the only moderately reliable morphological characteristic useful in distinguishing these two species is the direction of shell growth.

Discussion

The occurrence in Australia of *O. edulis* among a native *O. angasi* population has not hitherto been generally suspected, possibly because of similarities in shell characters. However, Tenison-Woods (1877) did think two species may be present and described briefly the external shell appearance of the Tasmanian *O. edulis* and *O. angasi*, but did not provide a morphological separation of the two. Stenzel (1971) and Harry (1985) also mentioned both species in their taxonomic studies of the genus *Ostrea* without identifying morphological differences between them. Sowerby (1871) considered that, of the two species, the sculpture of *O. angasi* was much less coarse and the upper valve more convex. Among the samples collected by us, the two sympatric species are difficult to differentiate individually in terms of shell characteristics. For example, *O. edulis* individuals from Oyster Harbour, when compared with sympatric *O. angasi*, do not have a more convex right valve, as suggested by Sowerby (1871). However, in general, *O. angasi* is slightly prosogyrous, whereas *O. edulis* is distinctively opisthogyrous. The former also has denser flaky lamellae on the margin of the right valve.

Previous studies have also shown it to be difficult to distinguish between *O. edulis* and *O. angasi* in terms of allozyme genetics and karyology. Blanc and Jaziri (1990)

compared 17 enzyme loci between the two species, since *O. angasi* was introduced experimentally into France from Australia. These authors showed that no locus was diagnostic and that no single locus could be considered specific for *O. angasi*. The patterns of karyotype, C-band and silver-stained nucleolus organizer regions of *O. angasi* from Port Lincoln, SA, are also very similar to those of European *O. edulis* (Li and Havenhand 1997). Not until recently has *O. angasi* from NSW and Tasmania been differentiated from French and Irish *O. edulis* in terms of a *16S* sequence divergence value of 0.67% (Jozefowicz and O'Foighil 1998). This genetic difference value was the lowest compared with other species pairs of the genus *Ostrea*. These results are confirmed herein (0.83%).

The *16S O. edulis* dataset obtained in the present study suggests an introduction of this species from Europe. The studied Albany 6 individual has a partial *16S* sequence identical to that of *O. edulis* from France and Ireland (Jozefowicz and O'Foighil 1998). However, comparisons of population genetics (e.g. *CO1* sequences of *O. edulis* individuals from the north-eastern Atlantic and the Mediterranean) are required to identify the origin of the introduced Albany *O. edulis*. Partial *16S* sequences of *O. angasi* from Albany have one consistent transition site compared with individuals from St Helens, Tasmania, and Pambula, NSW (Jozefowicz and O'Foighil 1998). This shows that the *O. angasi* populations in south-western and south-eastern Australian waters are distinct in terms of molecular genetics.

The present discovery of the European flat oyster *O. edulis* among native *O. angasi* stocks in Albany, WA, opens up the possibility of the former being introduced either accidentally or unofficially into Australia. There have been recent outbreaks of the parasitic protist *Bonamia ostreae* in *O. angasi* from Australia and, because this is usually considered to be specific to *O. edulis* in Europe and North America, is it possible that this pest was also brought into Australia with the non-native species?

Adlard (2000) reports that the first recorded instance of bonamiasis in the flat oysters of French waters was in 1979 (Comps *et al.* 1980). Significant mortalities of *O. edulis* have since been attributed to that disease in France, Spain, England, Ireland, Denmark, The Netherlands and North America (Balouet *et al.* 1983; Bucke and Feist 1985; Van Banning 1985; Elston *et al.* 1986). The disease is thought to have originated in North America, from where large numbers of oyster seed (*O. edulis*) were transferred from California to France prior to 1979 and, thence, spread to other European countries (Elston *et al.* 1986). Adlard (2000) also records that:

> '...in the summer of 1991, an ultrastructurally identical and genetically similar parasite to that found in New Zealand, was identified in the haemocytes of *O. angasi* in Port Phillip Bay and along the coast of Victoria, in southern and eastern Tasmania, and in south-western Western Australia, and has been associated with large scale mortalities of the host oyster. Thus, two distinct species of *Bonamia* are currently known, *Bonamia ostreae* in Europe and *Bonamia* sp. in Australasia.'

Adlard (2000) also considered the Australian species of *Bonamia* to be different from but ultrastructurally 'identical' to *B. ostreae* in Europe. Moreover, Bougrier *et al.* (1986), in France, showed that *O. angasi* is susceptible to *B. ostreae*. The earliest report, in late 1985, of bonamiasis in New Zealand was from *Tiostrea chilensis*. However, the disease was not reported from Australia (in *O. angasi*) until 1991. Therefore, it is possible that the initial outbreak of bonamiasis, in the case of Australia, may be correlated with the introduction of infected *O. edulis* sometime prior to 1991.

The results presented herein emphasise the value of molecular markers in: (*1*) discriminating morphologically plastic and closely related species; and (*2*) monitoring the consequences of species introduced into morphologically similar native stocks.

We caution against such introductions because of the likelihood of the importation of oyster diseases, such as bonamiasis, and of such impacts (as well as others) on native species.

Acknowledgments

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Review of the type material of Indo-West Pacific genus *Crassatina* (Mollusca : Bivalvia : Crassatellidae) with a description of two new species

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Abstract

The type material of eight Recent species of *Crassatina* is reviewed and illustrated. Two new species are described, *Crassatina rikai* n. sp. and *Crassatina suduirauti* n. sp., both from the Philippines, with the latter also known from northern Australia. All species occur in the Indo-West Pacific. Lectotypes are selected for *Crassatina ziczac* (Reeve, 1842), *Crassatina picta* (Adams & Reeve, 1850), *Crassatina corrugata* (Adams & Reeve, 1850), *Crassatina nana* (Adams & Reeve, 1850), *Crassatina pallida* (Adams & Reeve, 1850) and *Crassatina banksii* (Adams & Angas, 1863). *Talabrica* Iredale, 1924 is placed in the synonymy of *Crassatina* Kobelt, 1881. *Chattonia* Marwick, 1928 and *Salaputium* Iredale, 1924 are considered valid genera.

Introduction

An overview of crassatellid genera has been given by Chavan (1969) and Australian Crassatellidae were reviewed by Slack-Smith (1998). Of the three extant genera known from Australia, *Eucrassatela* Iredale, 1924 was revised by Darragh (1964), whereas *Talabrica* Iredale, 1924 and *Salaputium* Iredale, 1924 were treated by Lamprell and Whitehead (1992), Healy and Lamprell (1992) and Lamprell and Healy (1998). Tertiary species in the genus *Crassatella* Lamarck, 1799 were revised by Darragh (1964), whereas species of *Spissatella* Finlay, 1926 were treated by Pritchard (1903) and Darragh (1965). The present paper names two new species of the genus *Crassatina* Kobelt, 1881 and records the genus for the first time in Australian waters. The previously named Indo-Pacific species of *Crassatina* are reviewed herein and type specimens illustrated. Other crassatellid genera in the Indo-Pacific region include *Salaputium* Iredale, 1924, *Bathytormus* Stewart, 1930, *Chattonia* Marwick, 1928 and *Cypricardella* Hall, 1858, with both Tertiary and Recent species, and *Pachythaerus* Conrad, 1869, *Anthonya* Gabb, 1864 and *Oriocrassatella* Etherridge, 1907, with only Tertiary representatives.

Materials and methods

Institutional abbreviations and text conventions

AMS	The Australian Museum, Sydney
BMNH	The Natural History Museum, London
CSIRO	Commonwealth Scientific and Industrial Research Organisation
KL	Lamprell collection, presented to the Queensland Museum
MNHN	Muséum National d'Histoire Naturelle, Paris
QM	Queensland Museum, Brisbane
lv	left valve
pv	paired valves
rv	right valve

*Deceased 24 June 2003.

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Shell dimensions

For all material examined, length is the greatest distance between the anterior and posterior extremities, height was measured vertically from the umbo to the ventral margin and total width (inflation or breadth) is the greatest distance between the external surfaces of the paired valves. Unless otherwise stated, measurements are given for the largest specimens examined.

Taxonomy

Family **CRASSATELLIDAE** Férussac, 1822

Subquadrangular to trigonal, ovate anteriorly, truncated posteriorly. Concentrically ribbed to smooth. Ligament internal in pit, obliterating upper part of posterior cardinal tooth in left valve, narrow marginal nymphal ridge behind pit (modified from Chavan 1969).

Subfamily **CRASSATELLINAE** Férussac, 1822

Umbones prosogyrous or orthogyrous; cardinal teeth divergent. Resilium well developed (modified from Chavan 1969).

Genus ***Crassatina*** Kobelt, 1881

Type species: *Crassatella triquetra* 'Sowerby, 1843' = Reeve, 1842, by original designation.

Synonym: *Talabrica* Iredale, 1924: 204. Type species *Crassatella aurora* A. Adams & Angas, 1864; by original designation. New synonymy.

Description

Subtrigonal to subquadrate, small to moderate size (6–30 mm); umbones prosogyrous. Lunule and escutcheon narrow. Right valve with two cardinal teeth anterior to resilifer on prominent hinge plate; anterior cardinal tooth weak, short, confluent with anterodorsal margin below lunule; posterior cardinal tooth strong, transversely ridged on both faces. Two lateral teeth, anterior short, strong, separated from anterodorsal margin by groove; posterior lateral tooth twice length of anterior tooth, weak, confluent with posterodorsal margin. Left valve with two strong cardinal teeth anterior to resilifer, transversely ridged on inner faces, hinge plate prominent. Two lateral teeth, posterior short, weak, confluent with anterodorsal margin; posterior lateral tooth strong, separated from posterodorsal margin by groove. Internal margin finely crenulate.

Remarks

Iredale (1924) proposed the names *Talabrica* for the finely ribbed species *Crassatella aurora* A. Adams & Angas, 1863 and *Salaputium* for the coarsely ribbed *Crassatella fulvida* Angas, 1871 without clearly defining diagnostic characters of either genus. Shell macrosculpture appears to be the primary reason for Iredale's separation of the two genera. Cotton (1961) separated *Talabrica* and *Salaputium* from other Crassatellidae on the basis of shell size alone. Species that have been placed in *Talabrica* and *Salaputium* have diverse ornamentation and size. Species of *Salaputium* differ from *Crassatina* and *Talabrica*, in having a relatively small resilial pit and a vertical, discontinuous posterior cardinal tooth (Fig. 1B). The similarity of the hinge characters, including the anteriorly oblique, continuous posterior cardinal tooth and larger resilial pit in both *Crassatina* and *Talabrica* species (Fig. 1A, C), suggest that separation of these latter two genus-group names is not warranted.

Species previously assigned to *Talabrica* are *Talabrica aurora* (A. Adams & Angas, 1864), Tasmania and Victoria, *Talabrica fulvida* (Angas, 1871), New South Wales

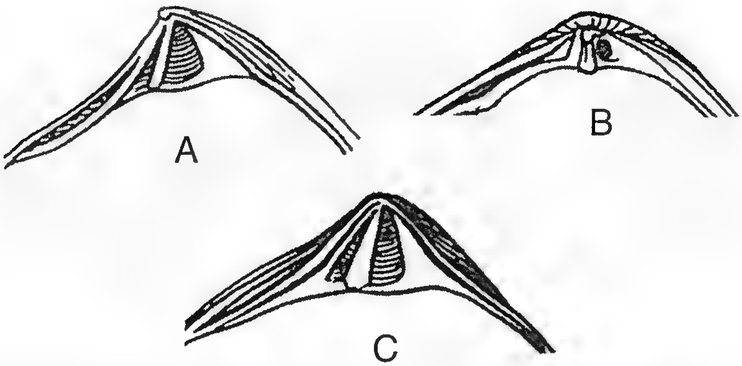

Fig. 1. Right valve hinges. *A*, *Crassatina* sp. cf. *bronni* (Wood); *B*, *Salaputium fulvidum* (Angas); *C*, *Talabraca aurora* (Adams and Angas) (slightly modified from Chavan 1969).

(Lamprell and Whitehead 1992: pl. 27, figs 177, 179) and *Talabrica donharrisi* (Healy & Lamprell, 1992: 95), Queensland. These taxa are not dealt with further in this review.

Although Chavan (1969) used *Chattonia* as a subgenus of *Crassatina*, *Chattonia* is treated here as a distinct genus for species with smooth valve margins and in which the ligamentary ridge and posterior laterals are separated (valve margins crenulate and ligamentary ridge in prolongation of the laterals in *Crassatina* species).

Crassatina suduirauti n. sp.

Fig. 2*A*–*C*, Table 1

Crassatina ziczac Slack-Smith, 1998: 326, fig. 8, 14E (not Reeve, 1842).

Material examined

Holotype. Philippine Islands, S of Balingasag Island, 8°45′N, 124°47′E, 0.5 km, 160–180 m, E. Guillot de Suduiraut, 1997, sand, in tangle nets, AMS C.400939 (1pv).

Paratype. Same data as holotype, MNHN (1pv); CSIRO Stn 40, 18°83.4′S, 147°70.2′E, N Queensland, 60 m, 4 Sep. 1997, BMNH 20010209 (1pv); CSIRO stn 41, 18°82.2′S, 147°69.8′E, 70 m, N Queensland, 4 Sep. 1997, QM MO.69798 (1pv).

Other material examined. **Philippine Islands**. Bohol Island, marrow collection, purchased from dealer (1pv). **Australia**. CSIRO stn 44, 18°80′S, 147°74′E, 62 m, N Queensland, 9 Apr. 1997, KL (1pv); CSIRO stn 51, 18°90.2′S, 147°88.1′E, 76 m, N Queensland, 9 Apr. 1997, KL (1pv); trawled off Pompey Reef, N of Swains Reef, Queensland, KL, from dealer (1pv, 1lv).

Description

Shell moderately large for genus, to 26 mm in length. Sub-quadrate, solid, equivalve, moderately inflated, inequilateral; umbones situated anteriorly, prosogyrate; anterodorsal margin short, narrowly rounded terminally; ventral margin very slightly convex, very narrowly rounded at posterior termination; posterior margin vertical, straight, angulate at posterior dorsal termination; posterodorsal margin slightly convex. Lunule narrow, impressed, lanceolate, radially striate. Ligament impressed, radially striate, defined by strong surrounding posterodorsal ridge; well-defined furrow extends from umbones to one-third of posterior margin. Sculpture of numerous, coarse, flattened concentric ribs (36+), interstices narrow, terminating at posterodorsal ridge. Anterior muscle adductor scar reniform, posterior adductor scar ovate. Pallial line well defined, pallial sinus diminutive.

Table 1. Shell dimensions of type material of *Crassatina suduirauti* n. sp.

	Length (mm)	Height (mm)	Width (pv) (mm)
Holotype			
AMS C.400939	24.5	21.0	14.3
Paratypes			
MNHN	26.0	23.0	13.9
BMNH 20010209	21.0	17.9	10.5
QM MO.69798	19.2	16.5	9.5

Internal margin densely crenulate, stronger ventrally. External colour white with orange tent-shaped markings and two radial rays of broken brown markings and unbroken lines extending medially from ventral margin to umbones; lunule and escutcheon with rose-coloured stitch-like patterned rays. Internally white with oblique rose ray posteriorly.

Distribution and habitat

Philippine Islands and Queensland, 60–180 m, in coarse sand.

Remarks

Crassatina suduirauti n. sp. is similar to *Crassatina ziczac* (Fig. 2*G–I*) in size and habitat, differing in its more quadrate profile (rather triangular in *C. ziczac*), the wider, straighter posterior margin, the straight to slightly convex ventral margin and the more anteriorly situated umbones (almost central in *C. ziczac*). *Crassatina picta* (Fig. 2*J–L*) has much coarser commarginal sculpture, centrally situated umbones and a strongly convex ventral margin (anteriorly situated umbones and straight to moderately convex ventral margin in *C. suduirauti*). *Crassatina nana* (Fig. 3*D–F*) is more ovate in profile and lacks the angulate outline of *C. suduirauti*. *Crassatina corrugata* (Fig. 3*A–C*) is similar to *C. suduirauti* in shape, but can be readily separated by the coarse, corrugated sculpture (coarse, flattened ribs in *C. suduirauti*).

Etymology

Named for E. Guillot de Suduiraut who donated material used in the present study.

Crassatina rikae n. sp.

Fig. 2*D–F*, Table 2

Material examined

Holotype. Aliguay Island, 8°35′N, 123°20′E, N of Dipolog, N Mindanao, Philippine Islands, R. De Donder-Goethaels, 150–300 m, trawled by pan-boats, Jun. 2000, AMS C.400938 (1pv).

Paratypes. Same data as holotype QM MO.69799 (2 pv); BMNH 20010208 (1pv), AMS C.204868 (1pv); MNHN (2pv); KL (11pv).

Description

Shell small, to 14.7 mm in length. Sub-quadrate, solid, equivalve, inequilateral, umbones situated anteriorly; moderately inflated; prosogyrate; anterodorsal margin short, narrowly rounded terminally; ventral margin very slightly convex, very narrowly rounded at

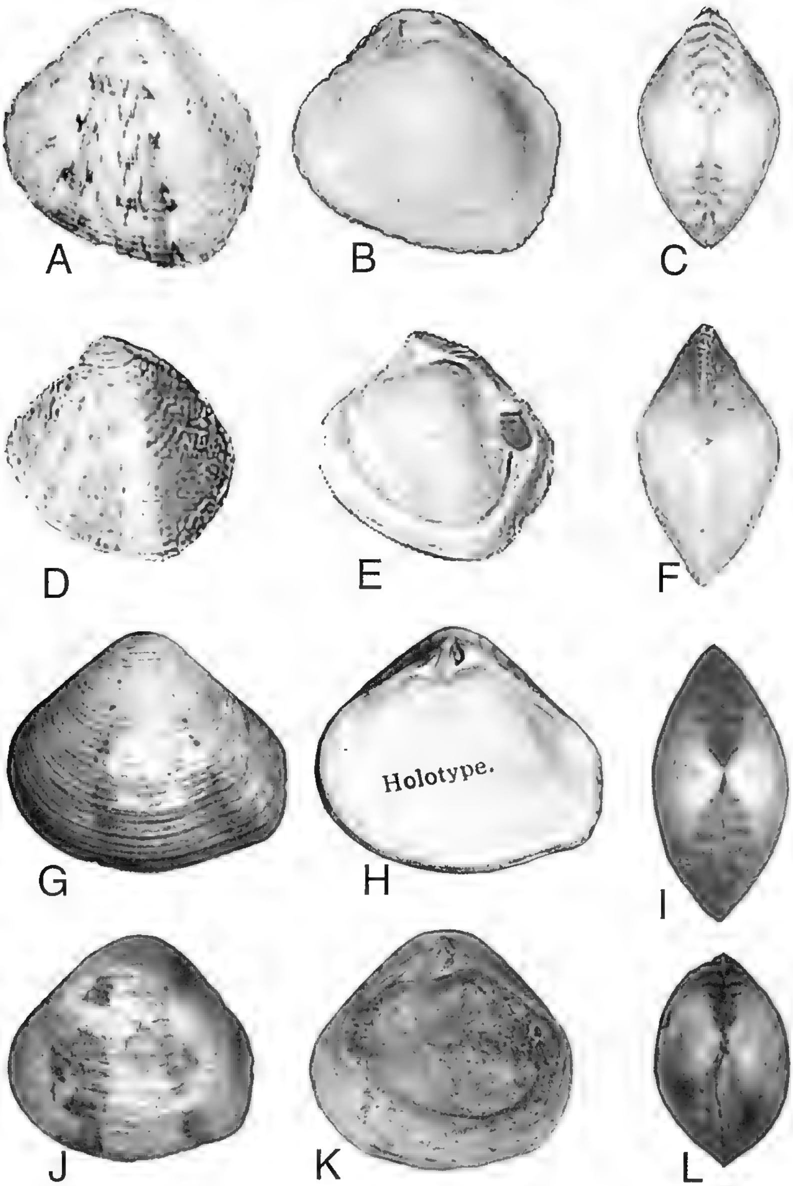

Fig. 2. *A–C*, *Crassatina suduirauti* n. sp. Holotype, length 24.5 mm, height 21.0 mm, width pv 14.3 mm. *A*, External view of lv; *B*, internal view of rv; *C*, dorsal view of pv (AMS C.400939). *D–F*, *Crassatina rikae* n. sp. Holotype, length 14.6 mm, height 13.6 mm, width pv 8.3 mm. *D*, External view of lv; *E*, internal view of rv; *F*, dorsal view of pv (AMS C.400938). *G–I*, *Crassatina ziczac* (Reeve, 1842). Lectotype, length 25.5 mm, height 20.3 mm, width pv 2.4 mm. *G*, External view of lv; *H*, internal view of rv; *I*, dorsal view of pv (BMNH 1953.4.15.5). *J–L*, *Crassatina picta* (Adams & Reeve, 1850). Lectotype, length 16.1 mm, height 14.7 mm, width pv 10.3 mm. *J*, External view of lv; *K*, internal view of rv; *L*, dorsal view of pv (BMNH 1996439/1).

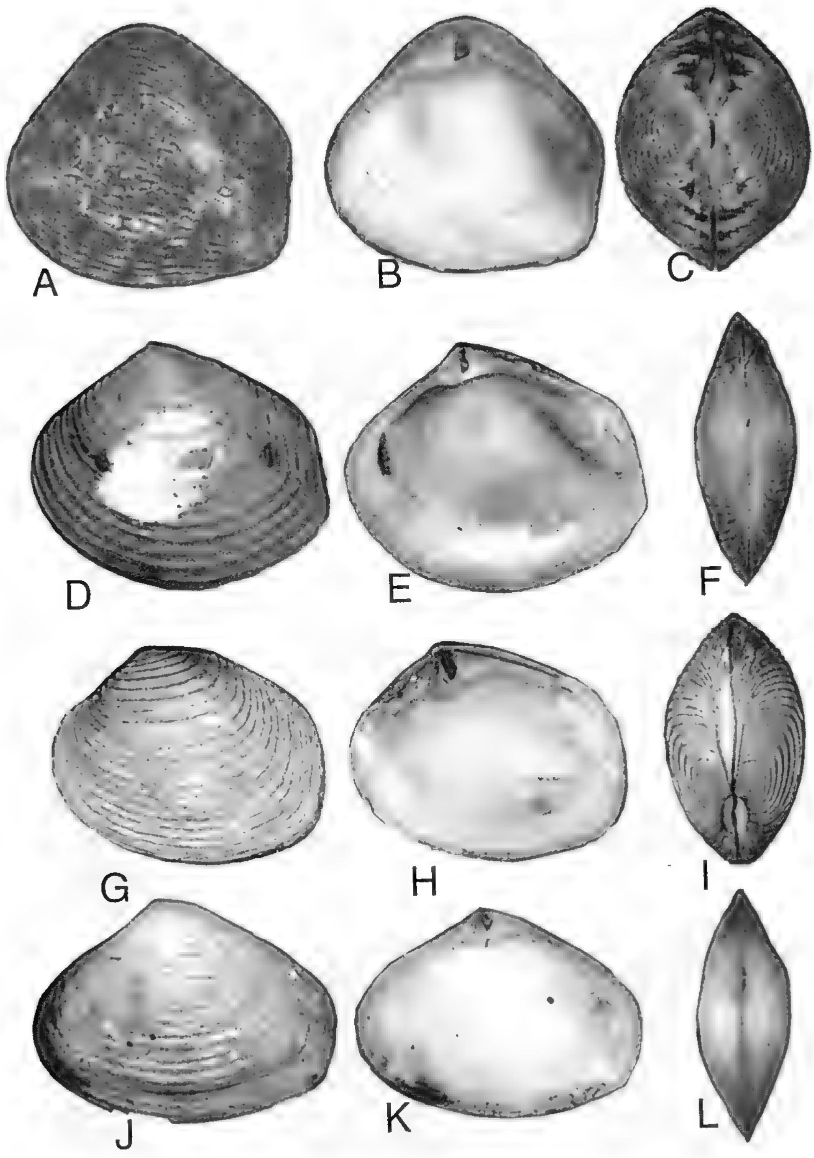

Fig. 3. *A–C, Crassatina corrugata* (Adams & Reeve, 1850). Lectotype, length 18.6 mm, height 17.2 mm, width pv 13.5 mm. *A*, External view of lv; *B*, internal view of rv; *C*, dorsal view of pv (BMNH 20010401). *D–F, Crassatina nana* (Adams & Reeve, 1850). Lectotype, length 16.6 mm, height 14.3 mm, width pv 6.1 mm. *D*, External view of lv; *E*, internal view of rv; *F*, dorsal view of pv (BMNH 1878.10.16.8 (Pt)). *G–I, Crassatina pallida* (Adams & Reeve, 1850). Lectotype, length 28.1 mm, height 22.5 mm, width pv 15.5 mm. *G*, External view of lv; *H*, internal view of rv; *I*, dorsal view of pv (BMNH 20010402). *J–L, Crassatina banksii* (Adams & Angas, 1863). Lectotype, length 16.3 mm, height 12.0 mm, width pv 6.4 mm. *J*, External view of lv; *K*, internal view of rv; *L*, external view rv.

Table 2. Shell dimensions of type material of *Crassatina rikae* n.sp.

	Length (mm)	Height (mm)	Width (pv) (mm)
Holotype			
AMS C.400938	14.6	13.6	8.3
Paratypes			
AMS C.204868	14.5	13.5	8.5
BMNH 20010208	15.2	12.5	7.9
QM MO.69799	12.5	11.3	7.0
MNHN	12.8	11.8	7.5
	14.5	12.4	8.9
	12.6	11.2	7.0

posterior termination; posterior margin vertically straight, angulate at posterodorsal termination; posterodorsal margin slightly convex. Lunule impressed, widely lanceolate, radially striate. Ligament impressed, radially striate, defined by strong surrounding posterodorsal ridge. Sculpture of numerous (24+) coarse, flatly rounded, upturned concentric ribs, interstices approximately half the width of concentric ribs, becoming obscure at the posterior one-third of the shell. Anterior adductor scar reniform, posterior adductor obovate. Pallial line well defined, pallial sinus diminutive. Internal margin weakly but densely crenulate, stronger ventrally. Externally white, with broken radial orange rays extending from umbones to ventral margin, posterior one-third rose coloured, sometimes with concentric darker orange rays and white background; lunule white; escutcheon rose coloured. Internally white, rose posteriorly, some external colour visible internally.

Distribution and habitat

N Mindanao, Philippine Islands, 150–300 m.

Remarks

Crassatina rickae n. sp. is most similar to *Crassatina suduirauti* (Figs 1*A*–*C*), in shape and colour. The sharper, narrower umbones in *C. rickae* and the widely lanceolate, as opposed to narrowly lanceolate, lunule are characteristics that separate *C. suduirauti* from *C. rickae*. *Crassatina rickae* has 24+ coarse, weakly rounded, upturned concentric ribs with interstices approximately half the width of the ribs, which become obscure at the posterior one-third of the shell, whereas *C. suduirauti* has numerous, coarse, flattened concentric ribs (36+) with narrow interstices terminating at the posterodorsal ridge. The lack of the rose stitch-like pattern posteriorly at the escutcheon and the medial pattern in *C. suduirauti* also help to separate the species. *Crassatina rickae* can be readily separated from other *Crassatina* species by its more quadrate shape and much smaller size.

Etymology

Named for Mrs Rika De Donder-Goethaels, who supplied material used in the present study.

Table 3. Shell dimensions of type material of *Crassatina ziczac* (Reeve, 1842)

	Length (mm)	Height (mm)	Width (pv) (mm)
Lectotype			
BMNH 1953.4.15.5	25.5	21.8	12.5
Paralectotypes			
BMNH 1953.4.15.6-7	26.6	20.3	12.4
	22.5	19.9	11.5

Crassatina ziczac (Reeve, 1842)

Fig. 2*G–I*, Table 3

Crassatella ziczac Reeve, 1842: 45; Reeve, 1843: 1, pl. 3, fig. 13.

Material examined

Holotype. Island off Corrigidor, Philippine Islands; specimen figured by Reeve, here selected as lectotype (Fig. 2*G–I*, specimen marked internally 'holotype' BMNH 1953.4.15.5; 1pv).

Paralectotypes. Same data as lectotype, BMNH 1953.4.15.6–7; two unfigured syntypes.

Diagnostic characteristics

Shell length to 26.6 mm. Trigonal, solid, equivalve, equilateral, umbones situated centrally, moderately inflated, narrowly rounded, prosogyrate; antero- and posterodorsal margins of equal length, steeply sloping, rounded anteriorly, angulate posteriorly; ventral margin convex, sharply rounded at posterior termination; posterior margin vertically straight. Lunule long, lanceolate, radially striate, impressed. Ligament radially striate, impressed, defined by strong surrounding posterodorsal ridge. An ill-defined furrow extends from umbones to ventral margin, terminating at posterior angulate margin. Sculpture of numerous (37+) low, rounded, upturned concentric ribs, interstices of equal width. Anterior muscle adductor scar reniform, posterior adductor scar obovate. Pallial line well defined, pallial sinus diminutive. Internal margin weakly but densely crenulate. Externally white with two broken radial orange rays extending medially to ventral margin, lunule and escutcheon with rose stitch pattern crossing both valves. Internally glossy white, rose posteriorly.

Remarks

The more triangular shape and narrower angulate posterior margin distinguish *C. ziczac* from *C. suduirauti* (Fig. 2*A–C*), which is of similar size and shape. *Crassatina picta* (Fig. 2*J–L*) and *C. corrugata* (Fig. 3*A–C*), although similar in shape, can be separated by the very coarse concentric ribs and smaller size in *C. picta* and oblique, corrugated ribbing in *C. corrugata*.

Crassatina picta (Adams & Reeve, 1850).

Figs 1*J–L*, Table 4

Crassatella picta Adams & Reeve, 1850: 82, pl. 23, fig. 6.

Material examined

Type material. Philippine Islands. Syntype figured by Reeve, here selected as lectotype BMNH 1996439/1 (Fig. 2*J–L*). Unfigured syntypes, same data as lectotype BMNH 1996439/2–5 (4pv).

Table 4. Shell dimensions of type material of *Crassatina picta* (Adams & Reeve, 1842)

	Length (mm)	Height (mm)	Width (pv) (mm)
Lectotype			
BMNH 1996439/1	16.1	14.7	10.3
Paralectotypes			
BMNH 1996439/2-5	11.6	11.7	8.5
	11.1	9.7	5.9
	8.8	7.2	4.0
	6.5	5.5	3.2

Diagnostic characteristics

Shell length to 16.1 mm. Trigonal, solid; equivalve, equilateral, umbones inflated, centrally situated; prosogyrate; anterodorsal margin slightly longer than posterodorsal margin, both steeply sloping, rounded anteriorly, angulate posteriorly; ventral margin convex, sharply rounded at posterior termination; posterior margin vertically straight. Lunule long, lanceolate, radially striate, impressed. Ligament radially striate, impressed, oblique, defined by strong surrounding posterodorsal ridge. Sculpture of (15+) coarse, rounded, upturned concentric ribs, becoming obscure posteriorly; interstices of equal width. Anterior muscle adductor scar reniform, posterior adductor scar obovate. Pallial line well defined; pallial sinus diminutive. Internal margin obsoletely crenulate, stronger ventrally. Externally white with blotches and broken radial orange rays extending medially from umbones to ventral margin, lunule with a rose stitch pattern; escutcheon tan. Internally dull white, some rose posteriorly.

Remarks

The smaller size, widely spaced and fewer concentric ribs and greater inflation distinguish *Crassatina picta* from *C. ziczac* (Fig. 2*G–I*), *C. nana* (Fig. 3*D–F*), *C. pallida* (Fig. 3*G–I*), *C. banksii* (Fig. 3*J–L*), *C. suduirauti* (Fig. 2*A–C*) and *C. rikai* (Fig. 2*D–F*); the wider and non-corrugated concentric ribs distinguish it from *C. corrugata* (Fig. 3*J–L*).

Crassatina corrugata (Adams & Reeve, 1850)

Fig. 3*A–C*, Table 5

Crassatella corrugata Adams & Reeve, 1850: 82, pl. 23, fig. 7.

Material examined

Type material. Sooloo Sea. Voyage of the Samarang. BMNH 20010401, syntype, 1pv figured by Reeve and marked internally A, here selected as lectotype (Fig. 2*J–L*). Unfigured syntype, 1pv internally marked B, same data as lectotype.

Table 5. Shell dimensions of type material of *Crassatina corrugata* (Adams & Reeve, 1850)

	Length (mm)	Height (mm)	Width (pv) (mm)
Lectotype A			
BMNH 20010401(pt)	18.6	17.2	13.5
Paralectotype B			
BMNH 20010401(pt)	17.3	17.0	13.0

Diagnostic characteristics

Shell length to 18.6 mm. Trigonal, solid, equivalve, equilateral; umbones centrally situated, inflated, rounded, prosogyrate; anterodorsal margin slightly shorter than posterodorsal, both steeply sloping, rounded anteriorly, angulate posteriorly; ventral margin convex, sharply rounded at posterior termination; posterior margin vertically straight. Lunule short, lanceolate, radially striate, impressed. Ligament radially striate, short, impressed, defined by strong surrounding posterodorsal ridge. Sculpture of (40+) rounded, upturned, oblique, corrugated, concentric ribs; interstices of equal width. Anterior muscle adductor scar reniform, posterior adductor scar obovate. Pallial line well defined, pallial sinus diminutive. Internal margin crenulations obsolete, stronger ventrally. Externally white with dense blotches and broken zigzag patterns extending over whole surface; lunule and escutcheon with rose stich-pattern. Internally glossy white, some purple posteriorly.

Remarks

The corrugated concentric, oblique ribs and greater inflation distinguish *Crassatina corrugata* from *C. ziczac* (Fig. 2*G–I*), *C. nana* (Fig. 3*D–F*), *C. pallida* (Fig. 3*G–I*), *C. banksii* Fig. 3*J–L*), *C. suduirauti* (Fig. 2*A–C*), *C. rikai* (Fig. 2*D–F*) and *C. picta* (Fig. 2*J–L*).

Crassatina nana (Adams & Reeve, 1850)

Fig. 3*D–F*, Table 6

Crassatella nana Adams & Reeve, 1850: 82, pl. 23, fig. 2.

Material examined

Type material. Eastern Seas (Indo-West Pacific). Voyage of the Samarang, BMNH 1878.10.16.8: 1pv. Notes with material borrowed from the BMNH dated 8.9.99 state 'None of these match the figure (pl. 23, fig 2) for size or patterning (*trifasciata* stated in description) may not be this species at all'. Another label, '... 878.10.16.8 is the registration number for 8 species donated by J.G. Jeffreys. The specimen supposedly marked 'MC' is not with this lot and has not been found therefore we believe this is not type material. Sept 2001. J.P.' (= Ms Joan Pickering, curatorial assistant, BMNH). However, in the absence of type material, and after examination of the available material and comparison with Reeve's figure and description, the specimen marked internally 'A' (figs 2*D–F*) is here selected as a neotype in accordance with ICZN (1999) 75.3.2–4.

Diagnostic characteristics

Shell length to 16.8 mm. Elongate–triangular, solid, equivalve, inequilateral, umbones situated slightly anterior of centre; narrow, prosogyrate; antero- and posterodorsal margins approximately equal size, moderately sloping, rounded anteriorly, angulate posteriorly;

Table 6. Shell dimensions of type material of *Crassatina nana* (Adams & Reeve, 1850)

	Length (mm)	Height (mm)	Width (pv) (mm)
Neotype BMNH 1878.10.16.8	6.6	14.3	6.1
Specimen marked A BMNH 1878.10.16.8	14.5	12.8	5.4
Second specimen in lot of six unpaired valves	9.1	8.0	1.7

ventral margin broadly convex, sharply rounded at posterior termination; posterior margin vertically straight. Lunule lanceolate, narrow, radially striate, impressed. Ligament narrow, radially striate, impressed, defined by strong surrounding posterodorsal ridge. Sculpture of (26+) rounded, upturned concentric ribs; interstices of equal width. Anterior adductor scar reniform, posterior adductor scar ovate. Pallial line well defined, pallial sinus diminutive, internal margin with ill-defined crenulations. Externally pale brown. Internally off-white, pale brown medially.

Remarks

The more elongate shape and narrower profile distinguish *Crassatina nana* from the more triangular *C. corrugata* (Fig. 2*A–C*), *C. ziczac* (Fig. 2*G–I*), *C. picta* (Fig. 2*J–L*), *C. suduirauti* (Fig. 2*A–C*) and *C. rikai* (Fig. 2*D–F*). *Crassatina nana* can be distinguished from the larger *C. pallida* (Fig. 3*G–I*) and equally small sized *C. banksii* (Fig. 3*J–L*) by its more angulate, straighter posterior margin (widely convex in *C. pallida*, narrowly convex in *C. banksi*).

Crassatina pallida (Adams & Reeve, 1850)

Fig. 3*G–I*, Table 7

Crassatella pallida Adams & Reeve, 1850: 82, pl.23, fig. 9.

Material examined

Type material. China Sea. Voyage of the Samarang. Syntype figured by Reeve here selected as lectotype (Fig. 3*G–I*) BMNH 20010402 (1pv).

Other material examined. Same data as syntype, with the notation 'A non-type specimen 1878.1.28.35 was removed from this board and put in general collection. Sept. 2001'. This specimen, BMNH 1878.1.28.35, has not been found.

Diagnostic characteristics

Shell length to 28.0 mm. Elongate–ovate, solid, equivalve, inequilateral; umbones moderately inflated, situated one-third anteriorly, prosogyrate; anterodorsal margin short sloping, widely rounded at ventral termination; posterodorsal margin slightly convex narrowly rounded at posterior termination; posterior margin very slightly convex, upright, sharply rounded at ventral termination; ventral margin widely convex. Lunule lanceolate, narrow, radially striate, impressed. Ligament narrow, radially striate, impressed, wider on right valve, defined by strong surrounding posterodorsal ridge. Sculpture of (35+) upturned concentric ribs, interstices wider. Anterior muscle adductor scar reniform, posterior adductor scar obovate. Pallial line well-defined, pallial sinus diminutive, internal margin with ill-defined crenulations, stronger ventrally. Externally dirty white. Internally glossy white.

Table 7. Shell dimensions of type material of *Crassatina pallida* (Adams & Reeve, 1850)

	Length (mm)	Height (mm)	Width (pv) (mm)
Lectotype BMNH 20010402	28.1	22.5	15.5

Remarks

The more elongate and less triangular profile distinguish *Crassatina pallida* from the triangular *C. corrugata* (Fig. 3*A–C*), *C. ziczac* (Fig. 2*G–I*), *C. picta* (Fig. 3*J–L*), *C. suduirauti* (Fig. 2*A–C*) and *C. rikai* (Fig. 2*D–F*). *Crassatina nana* can be distinguished from the smaller *C. pallida* (Fig. 3*G–I*) and *C. banksii* (Fig. 3*J–L*) by its greater inflation and wide, slightly convex posterior margin (angulate posterior margin in *C. nana* and narrowly convex posterior margin in *C. banksii*).

Crassatina banksii (Adams & Angas, 1863)

Fig. 3*J–L*, Table 8.

Crassatella banksii Adams & Angas, 1863: 5: p. 427, pl. 37, fig. 16.

Material examined

Type material. Banks Straits, Tasmania, BMNH 1870.10.26.36 (1pv). Figured syntype here selected as lectotype (Fig. 3*J–L*).

Diagnostic characteristics

Shell length to 16.3 mm. Elongate–triangular, thin, equivalve, slightly inequilateral; umbones compressed, situated anterior of centre, prosogyrate; anterodorsal and posterodorsal margins of approximately equal size, moderately sloping, widely rounded anteriorly, angulate posteriorly; ventral margin widely convex, sharply rounded at posterior termination; posterior margin vertically straight. Lunule lanceolate, narrow, radially striate, impressed. Ligament narrow, radially striate, impressed, defined by strong surrounding posterodorsal ridge. Sculpture of (26+) rounded, upturned concentric ribs becoming oblique after posterior fold. Interstices narrower than ribs. Anterior muscle adductor scar reniform, posterior adductor scar obovate. Pallial line obscure, pallial sinus diminutive, internal margin weakly crenulate, better defined ventrally. Externally dirty white with two obscure radial light-brown rays medially. Internally glossy-white.

Remarks

Crassatina banksi can be distinguished from *C. nana* (Fig. 3*D–F*) and *C. pallida* (Fig. 3*G–I*), which are similar in profile, being more elongate and less triangular than the other species in the genus, by the narrowly convex posterior margin and oblique concentric sculpture at the postero-umbonal fold (posterior margin straight in *C. nana* and widely convex in *C. pallida*) and sculpture (26+ continuous concentric ribs in *C. banksi*, 35+ in *C. pallida*).

This species has apparently not been recollected in Tasmania or Bass Strait and may well be mislocalised. The other small southern Australian crassatellids are less elongate.

Table 8. Shell dimensions of type material of *Crassatina banksii* (Adams & Angas, 1863)

	Length (mm)	Height (mm)	Width (pv) (mm)
Lectotype BMNH 1870.10.26.36	16.3	12.0	6.4

Key to species

1.	Shell with oblique sculpture	2
	Shell without oblique sculpture	3
2.	Oblique sculpture over entire external surface	*Crassatina corrugata*
	Oblique sculpture posteriorly	*Crassatina banksii*
3.	Shell triangular, umbones centrally situated	4
	Shell not triangular, umbones situated anterior of centre	7
4.	Ventral margin steeply sloping posteriorly	6
	Ventral margin evenly rounded, not sloping posteriorly	5
5.	Interstices narrow, concentric ribs narrow	*Crassatina ziczac*
	Interstices wide, concentric ribs coarse	*Crassatina picta*
6.	Shell with posterior coloured radial ray	*Crassatina rikae*
	Shell without posterior coloured radial ray	*Crassatina suduirauti*
7.	Shell elongate-triangular, concentric sculpture coarse, even	*Crassatina nana*
	Shell elongate—ovate, concentric sculpture upturned dorsally	*Crassatina pallida*

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Spatial variability in reproductive behaviour of green-lipped mussel populations of northern New Zealand

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Abstract

The reproductive behaviour of four intertidal and two subtidal mussel populations were investigated within two spatial scales at Ninety Mile Beach, northern New Zealand, where large quantities of seed mussels are collected for aquaculture. Reproductive cycles were compared between intertidal and subtidal populations and among intertidal populations along a 90-km coastal area. Histological sections of mussel gonads were used to identify the reproductive state of individual mussels collected monthly between July 1998 and April 2000. Gonad indices were calculated for populations each month at each site. Frequency distributions of different gametogenic stages were plotted and differences in reproductive cycle among populations were identified. Mussel shell sizes were also recorded and compared among populations. Although all intertidal and subtidal populations had similar temporal variations in reproductive behaviour, spatial patterns among various sites revealed clear differences in reproductive cycles among populations. In particular, mussel shell size and gonad indices were higher for subtidal sites compared to their intertidal counterparts. Among intertidal mussel populations, the northernmost population had the highest maximum shell length, gonad indices and percentage ripe and spawning individuals, followed by two populations at the southern end of Ninety Mile Beach. A small mid-beach mussel population had the smallest mussels with the lowest gonad indices and few spawning mussels during the reproductive season. A prolonged spawning period was observed within the most reproductively active populations (two subtidal populations at the south end and one intertidal population at the north end of the beach) between June and December. However, the reproductive cycle of two intertidal populations at the south end of the beach indicated 2–3 spawning events during the same period. Differences in mussel shell size and reproductive behaviour among sites are likely to be related to variations in environmental conditions along Ninety Mile Beach.

Additional keywords: gonad cycle, histology, intertidal, *Perna canaliculus*, spat, spawning synchrony, subtidal.

Introduction

The biology of the commercially important green-lipped mussel, *Perna canaliculus*, has received considerable interest in recent years because the industry largely depends on >160 tonnes per year of wild mussel spat (attached to macroalgae) collected from Ninety Mile Beach in northern New Zealand to seed their farms (Jeffs *et al.* 1999). However, understanding the basic biology of natural mussel populations is critical if mussel spat are to be utilised reliably in terms of their availability and arrival at coastal areas along Ninety Mile Beach. The reproductive behaviour of *Perna canaliculus* has been investigated for mussel-farm populations in Marlborough Sounds (Flaws 1975; Tortell 1976; Hickman *et al.* 1991; Buchanan 1998) and wild populations at Ninety Mile Beach (Alfaro *et al.* 2001). However, differences in environmental conditions, such as water temperature, salinity and food availability, make generalisations from one population to another difficult (Newell *et*

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al. 1982; Hickman *et al.* 1991; Snodden and Roberts 1997). The temporal variability in reproduction of mussels at Ninety Mile Beach, where the majority of New Zealand's mussel spat is collected, has been investigated previously (Alfaro *et al.* 2001). However, spatial variability in reproduction of mussel populations along the 90-km coastal stretch, as described herein, provides important additional information regarding the dynamics of gamete production in the area. These studies on the reproductive biology of *Perna canaliculus* are part of an ongoing, integrative research programme analysing larval behaviour, settlement and recruitment processes and adult mussel-bed population dynamics, which may contribute to the future sustainability of wild spat production from Ninety Mile Beach.

Study of the reproductive behaviour of various mussel populations within a given geographical area can provide valuable information on variability of reproductive efforts at different spatial scales. This information then can be used to aid predictions of patterns of spatfall supplies to coastal areas, which can be utilised for commercial purposes and environmental resource management. One way to describe the reproductive efforts of a population is by using a gonad index as a standardised measure of reproductive maturity (Kautsky 1982; Brown 1988; King *et al.* 1989; Borcherding 1991; Galinou-Mitsoudi and Sinis 1994). Seasonal variations in reproductive cycle can be obtained and compared among populations by quantifying the frequency of mussels within various reproductive stages in the populations at a given time (Kautsky 1982; Shafee 1989; Villalba 1995; Nichols 1996).

The aim of this study is to investigate differences in reproductive behaviour of *Perna canaliculus* populations within different habitats along Ninety Mile Beach, northern New Zealand. Reproductive patterns of four intertidal and two subtidal adult mussel populations from Scott Point to Ahipara Bay are examined and compared to address spatial variability.

Materials and methods

Six geographically distinct mussel populations likely to be affected by different environmental conditions were identified at Ninety Mile Beach, northern New Zealand. Four rocky, intertidal mussel populations were located at Tonatona Beach, Ungaunga Bay, The Bluff and Scott Point; whereas two subtidal populations were found at Wizard Rock and Blue House (Fig. 1). The Tonatona Beach and Ungaunga Bay populations are exposed to intermittent strong easterly swells from the prevailing easterly winds and northbound Westland current, as well as periodic sediment load disturbances from redistributed nearby sands. A mussel population at The Bluff (Fig. 1) is also exposed to both high wave action and sand load disturbances. The northernmost population at Scott Point experiences strong hydrodynamic regimes, but because of the extensive rock reef, the sediment load appears to be low in comparison with the other intertidal populations. The subtidal populations at Wizard Rock and Blue House are located ~8 km apart near Ahipara Bay and are in 13 and 15 m water depth respectively (Fig. 1).

Gonad maturity analyses from histological sections were carried out on mussel specimens from the six study sites at Ninety Mile Beach. Approximately 70 adult mussels (50 to 145 mm in greatest length) were collected monthly from each of the six sites. An attempt was made to sample all sites once a month, but collections were not possible during certain months owing to poor weather conditions, or during months when collections were prohibited by cultural traditions of native Maori land owners. Sampling took place from July 1998 to April 2000. Intertidal mussels were collected haphazardly during low tide; whereas subtidal mussels were dredged when weather conditions permitted, from which 70 mussels were selected haphazardly for study from the dredge. Immediately after collection, the mussels were measured across their greatest shell length, sectioned dorsoventrally through the mid-body and the tissues fixed in Bouin's solution. Mussel tissues were histologically processed and the resulting slides were analysed under a microscope according to techniques developed for this species (Alfaro *et al.* 2001). Gonad indices, based on gonad maturity, for each population were calculated following King *et al.* (1989) and Galinou-Mitsoudi and Sinis (1994) using the following formula:

$$G.\ I. = \frac{\text{(number in each stage) (rank of stage)}}{\text{total sample size}} \times 100$$

where the scoring system was:

Resting stage	0
Early development stage	1
Late development stage	2
Ripe stage	3
Spawning stage	2
Redevelopment stage	2
Spent stage	1

Frequency distribution graphs, including all developmental stages, were constructed to identify differences in gametogenic activity among the six sites investigated.

Statistical analyses

Mussel shell length and gonad index data were tested for any violations of the basic parametric statistical assumptions and no transformations were necessary. Repeated-measures designs, with a MANOVA approach and profile analysis methodology, were used on the mussel shell length and gonad index data to

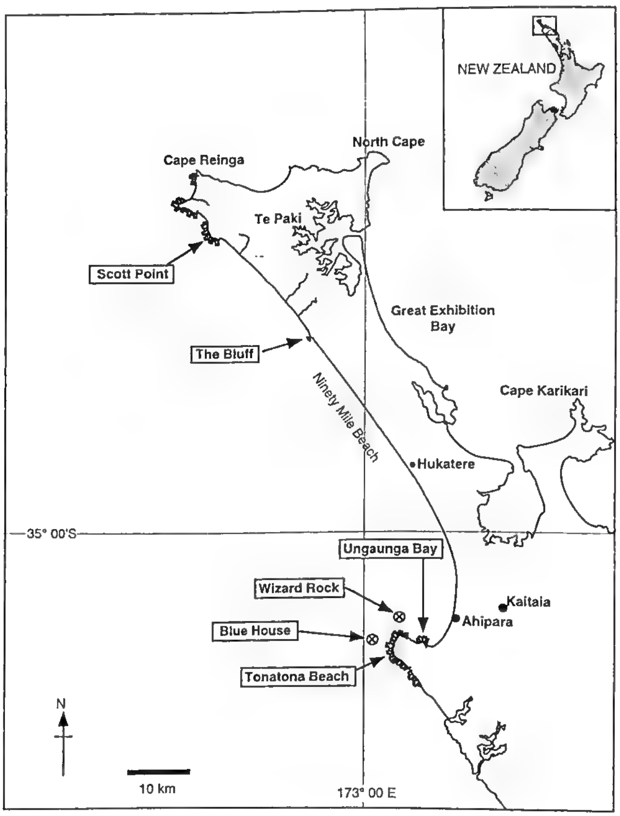

Fig. 1. Map of the study site at Ninety Mile Beach, northern New Zealand. Four intertidal (Tonatona Beach, Ungaunga Bay, The Bluff and Scott Point) and two subtidal (Wizard Rock and Blue House) mussel populations are shown.

test multivariate responses between intertidal and subtidal habitats and between southern and northern habitats. Thus, when comparing intertidal and subtidal habitats, two replicate intertidal sites and two replicate subtidal sites where used. Similarly, two replicate northern sites and two replicate southern sites were used in the southern *v.* northern habitat analyses. Using repeated-measures analyses made it possible to take into account the correlation among times sampled (dates), which avoided the problem of pseudoreplication, because measurements among dates were not independent (i.e. the same population was sampled over time). For this type of analysis, habitat and date were always fixed factors and the sites nested within habitats were random. When the repeated-measures data were analysed with MANOVA, the response variable for each level of the within-subject factor (date) was treated as a different dependent variable. These analyses allowed us to test whether the mean response vectors among the between-subject (habitat) levels were different. In order to satisfy conditions of MANOVA, equal sample sizes were achieved by only using sampling events that were shared by all sites in a given statistical test. In addition, the large sample sizes of individual mussels ensured powerful statistical analyses. The pattern of response of the date factor was analysed with profile analysis, which uses the contrasts or differences of adjacent date-pairs to detect significance of treatments and interactions (Scheiner and Gurevitch 1993). Individual ANOVAs, with Bonferroni α adjustments, were also conducted for each significance test to identify specific dates when treatment effects differed.

Results

Mussel shell length

Maximum shell length measurements of adult mussels from intertidal and subtidal sites at Ninety Mile Beach resulted in marked differences in mean maximum shell length among mussels from the six different sites. Generally, subtidal mussels were larger than intertidal mussels and mussels from Scott Point were consistently larger than mussels from all other intertidal sites. The Bluff had the smallest mussels of any site at Ninety Mile Beach throughout the study period (Fig. 2). Mean (± s.e.) maximum shell lengths for Tonatona

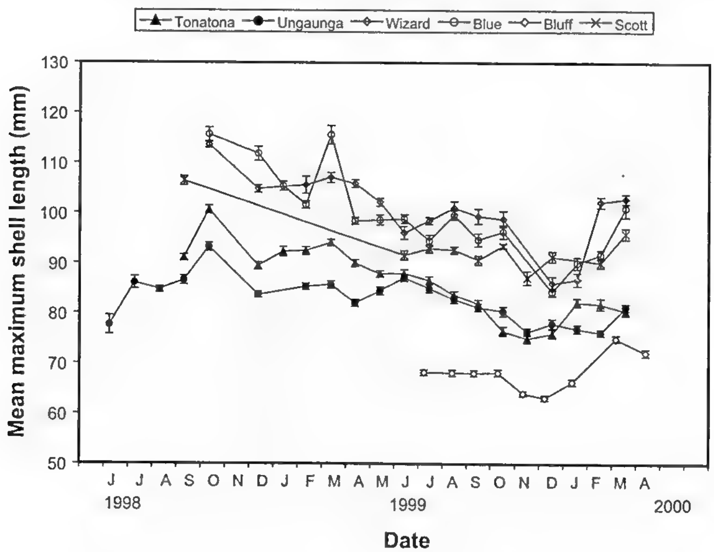

Fig. 2. Mean (± s.e.) maximum shell length of mussels within six adult mussel populations sampled monthly between July 1998 and April 2000. Means were calculated from 70 adult mussels on each date sampled within each site. Tonatona Beach, Ungaunga Bay, The Bluff and Scott Point represent four intertidal populations and Wizard Rock and Blue House constitute two subtidal mussel populations.

Beach, Ungaunga Bay, The Bluff, Scott Point, Wizard Rock and Blue House were 86 ± 0.3, 82 ± 0.2, 68 ± 0.2, 93 ± 0.3, 101 ± 0.4 and 99 ± 0.4 mm, respectively; and ranges of shell length were 60–116, 59–111, 50–88, 64–125, 71–145 and 70–142 mm, respectively. Results from repeated-measures MANOVAs, comparing mean maximum shell length between intertidal (Tonatona Beach and Ungaunga Bay) and subtidal (Wizard Rock and Blue House) habitats and between southern (Tonatona Beach and Ungaunga Bay) and northern (Scott Point and The Bluff) habitats, are shown in Table 1. Single Bonferroni-adjusted paired contrast ANOVAs for variables, which revealed significant group differences, also are shown in Table 1.

Female and male synchrony

Perna canaliculus is dioecious and, from our results, no major differences were observed in gonad indices and reproductive cycles between female and male mussels in any of the six sites studied, nor in months sampled between July 1998 and April 2000 (Figs 4–5, 7). This high level of reproductive synchrony allowed for female and male gonad indices to be pooled for further comparisons among sites and dates. Temporal variability in reproductive behaviour was remarkably similar among all sites and is reported elsewhere (Alfaro *et al.* 2001). Generally, populations showed higher levels of reproductive maturity and spawning between March and December and very little spawning outside this reproductive season. However, some differences in mussel reproductive behaviour were observed between habitats (Alfaro *et al.* 2001).

Table 1. Statistical analyses of maximum mussel shell length

A repeated-measures MANOVA (model III) was used to test multivariate responses between intertidal (Tonatona Beach and Ungaunga Bay) and subtidal (The Bluff, and Scott Point) habitats and, in a separate analysis, between southern (Tonatona Beach and Ungaunga Bay) and northern (The Bluff, and Scott Point) habitats. Profile analyses with contrasts between adjacent date pairs were conducted with individual ANOVAs and using Bonferroni α adjustments

	d.f.	m.s.	F	P	Significant contrasts
Intertidal *v.* subtidal habitats					
Between-subject					
Habitat	1	3628.15	52.42	0.019	
Error	2	69.22			
Within-subject					
Date	14	146.73	16.76	0.001	Jul/Aug, Aug/Sep, Sep/Oct, Oct/Dec
Habitat × date	14	19.60	2.24	0.034	
Error (Date)	28	8.76			
Southern *v.* northern habitats					
Between-subject					
Habitat	1	1.57	0.001	0.973	
Error	2	1109.34			
Within-subject					
Date	7	17.57	3.17	0.032	
Habitat × Date	7	13.76	2.48	0.070	Jul/Aug, Aug/Sep
Error (Date)	14	5.55			

Statistically significant contrasts between dates are shown on the right column (significant date pairs only occurred in 1999).

Intertidal v. *subtidal populations*

The reproductive behaviour of two intertidal mussel populations (Tonatona Beach and Ungaunga Bay) was compared to the reproductive behaviour of two nearby (~10 km) subtidal populations (Wizard Rock and Blue House) at the southern end of Ninety Mile Beach. Intertidal mussels consistently had lower gonad indices than subtidal mussels (Fig. 3). The mean (± s.e.) gonad index and range from Tonatona Beach mussels were 189 ± 8 and 144–259, whereas Ungaunga Bay mussels had a gonad index mean (± s.e.) and range of 173 ± 6 and 136–247. The frequency distribution of all reproductive stages for mussels within Tonatona Beach and Ungaunga Bay indicated similar reproductive cycles, although at Ungaunga Bay, a greater number of mussels were in the spent stage throughout the post-spawning periods (Fig. 4). Mussels from both intertidal sites showed two or three likely spawning events between June and November that were concurrent at both sites, followed by rapid gametogenesis until the end of the spawning season in December (Figs 3–4). Compared to the intertidal populations, the subtidal populations had gonad index means (± s.e.) and ranges of 220 ± 10 and 158–268 for Wizard Rock and 215 ± 8 and 161–277 for Blue House, respectively. Furthermore, intertidal mussel populations had greater numbers of mussels in the spent stage of development than subtidal populations before the end of the spawning season in November/December (Figs 4–5). Conversely, the percentage of ripe and spawning mussels was consistently higher for subtidal mussel populations than intertidal populations throughout the reproductive season (March to December) (Figs 4–5).

Repeated-measures MANOVA and profile analyses to test differences in gonad indices between intertidal (Tonatona Beach and Ungaunga Bay) and subtidal (Wizard Rock and Blue House) habitats among 15 months, between November 1998 and April 2000, are shown in Table 2. Repeated-measures ANOVAs to test differences in treatment effects between 14 paired-date contrasts also are shown in Table 2.

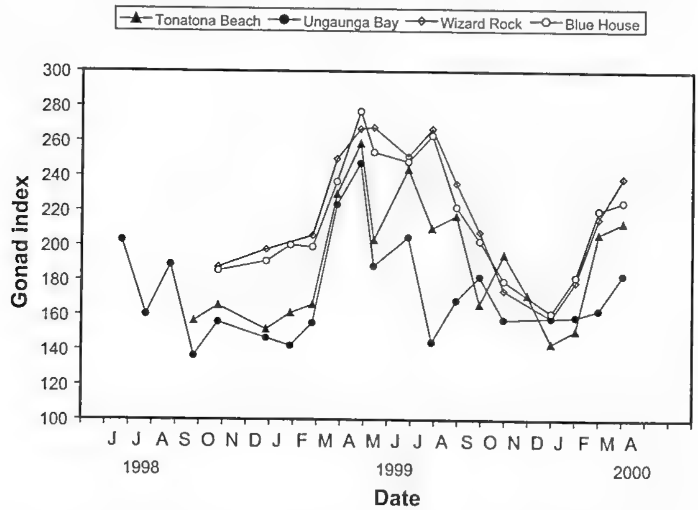

Fig. 3. Gonad indices for two intertidal (Tonatona Beach, Ungaunga Bay) and two subtidal (Wizard Rock and Blue House) mussel populations at Ninety Mile Beach. A total of 70 mussels were sampled on each date and within each site to calculate a gonad index at a given date and site.

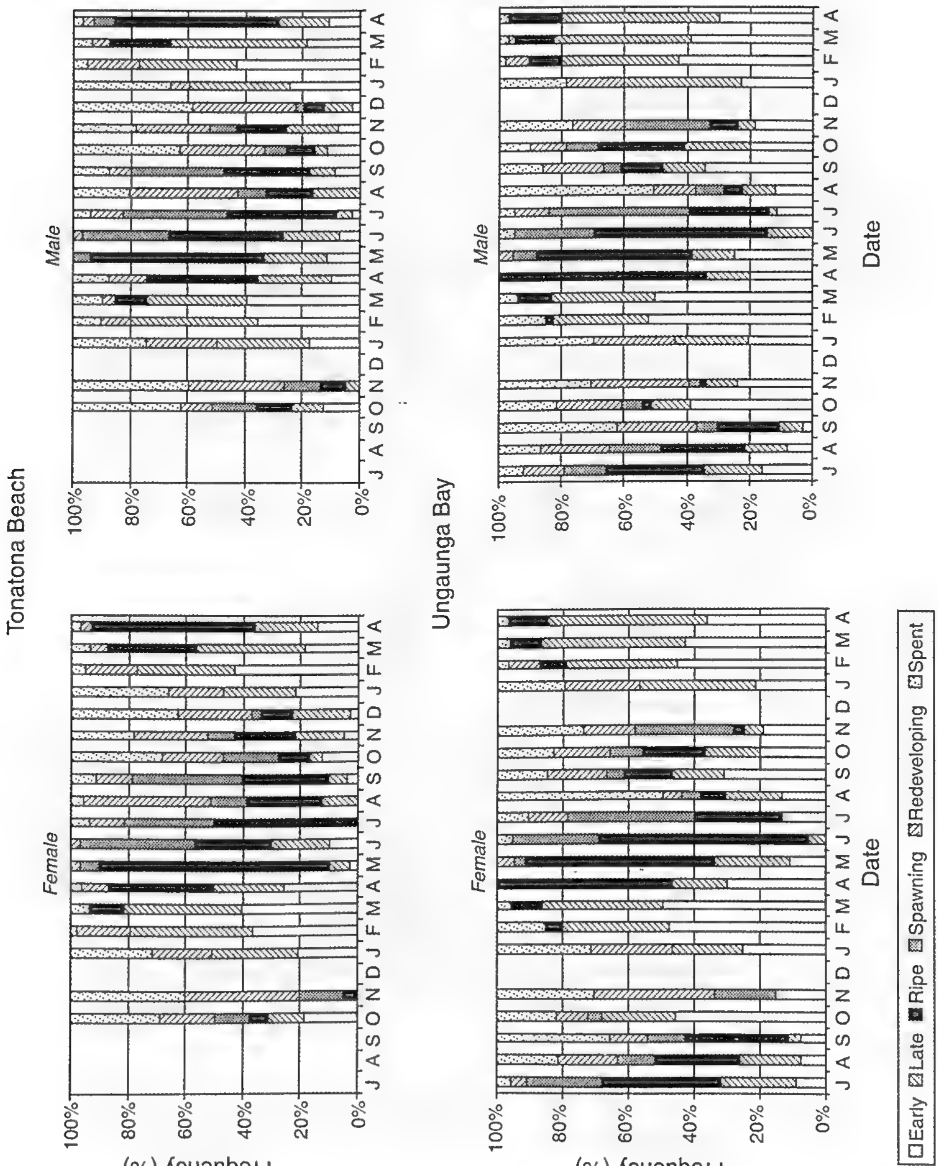

Fig. 4. Frequency distribution of six developmental stages (early development, late development, ripe, spawning, redeveloping and spent) of gonad reproductive state for female and male mussels at two intertidal sites (Tonatona Beach and Ungaunga Bay).

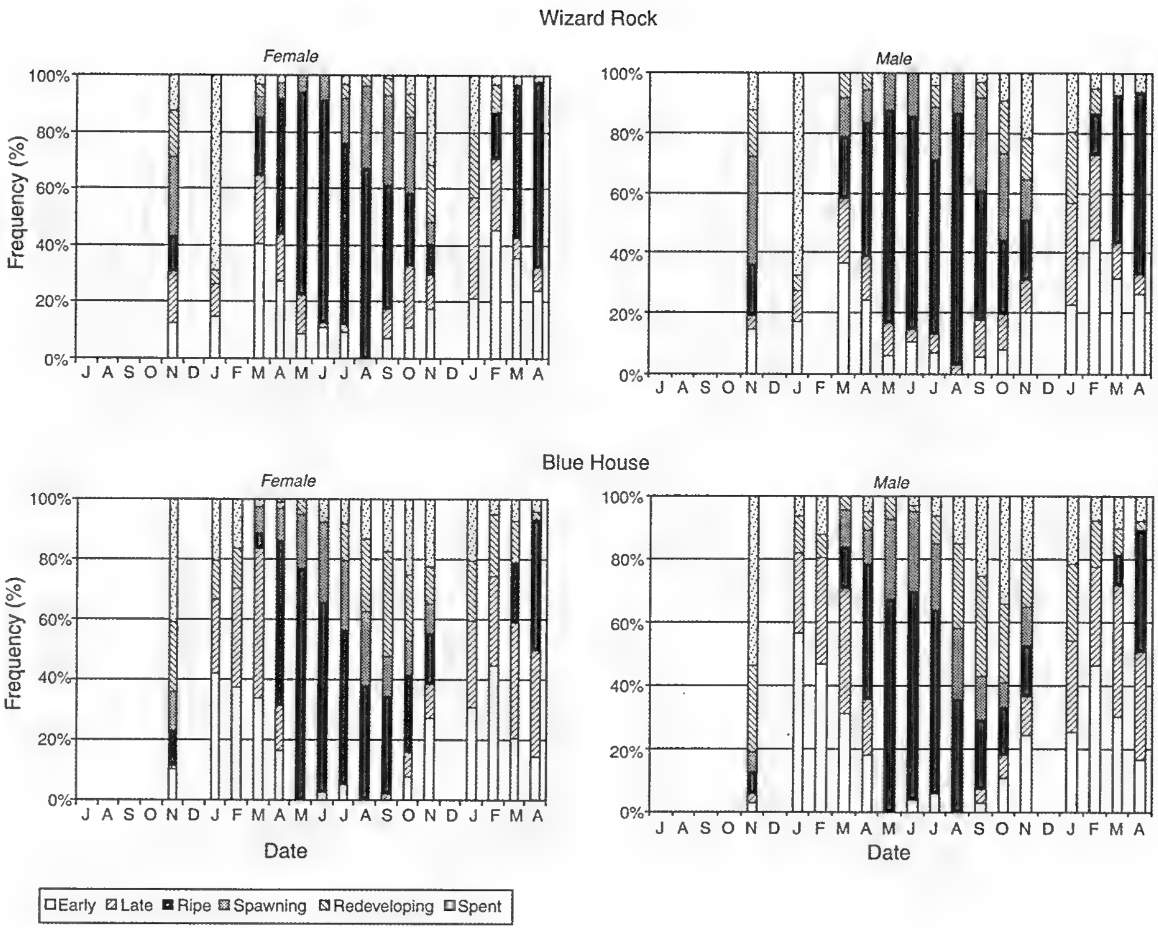

Fig. 5. Frequency distribution of six developmental stages (early development, late development, ripe, spawning, redeveloping and spent) of gonad reproductive state for female and male mussels at two subtidal sites (Wizard Rock and Blue House).

Table 2. Statistical analyses of mussel gonad index

A repeated-measures MANOVA (model III) was used to test multivariate responses between intertidal (Tonatona Beach and Ungaunga Bay) and subtidal (The Bluff, and Scott Point) habitats and, in a separate analysis, between southern (Tonatona Beach and Ungaunga Bay) and northern (The Bluff, and Scott Point) habitats. Profile analyses with contrasts between adjacent date pairs were conducted with individual ANOVAs and using Bonferroni α adjustments

	d.f.	m.s.	F	P	Significant contrasts
Intertidal *v.* subtidal habitats					
Between-subject					
Habitat	1	19279.06	22.32	0.042	
Error	2	863.71			
Within-subject					
Date	14	3965.90	41.41	0.001	Oct/Dec, Dec/Feb,
Habitat × Date	14	581.96	6.08	0.001	Feb/Mar, Apr/May,
Error (Date)	28	95.78			Jun/Jul, Dec/Jan
Southern *v.* northern habitats					
Between-subject					
Habitat	1	334.76	0.03	0.871	
Error	2	9881.36			
Within-subject					
Date	7	1694.58	5.17	0.004	
Habitat × Date	7	357.98	1.09	0.419	Jul/Aug, Aug/Sep
Error (Date)	14	327.76			

Statistically significant contrasts are shown on the right column (significant date pairs for intertidal *v.* subtidal habitats extend from 1998 to 2000, and occurred only in1999 for southern *v.* northern habitat comparisons).

Southern v. *northern populations*

Larger-scale comparisons in reproductive behaviour were conducted among southern (Tonatona Beach and Ungaunga Bay) and northern (The Bluff and Scott Point) intertidal

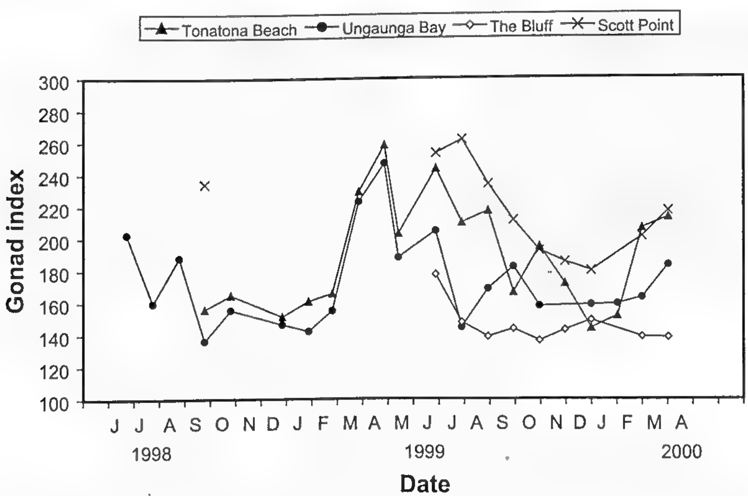

Fig. 6. Gonad indices for four intertidal mussel populations (Tonatona Beach, Ungaunga Bay, The Bluff and Scott Point) at Ninety Mile Beach. A total of 70 mussels were sampled on each date and within each site to calculate a gonad index at a given date and site.

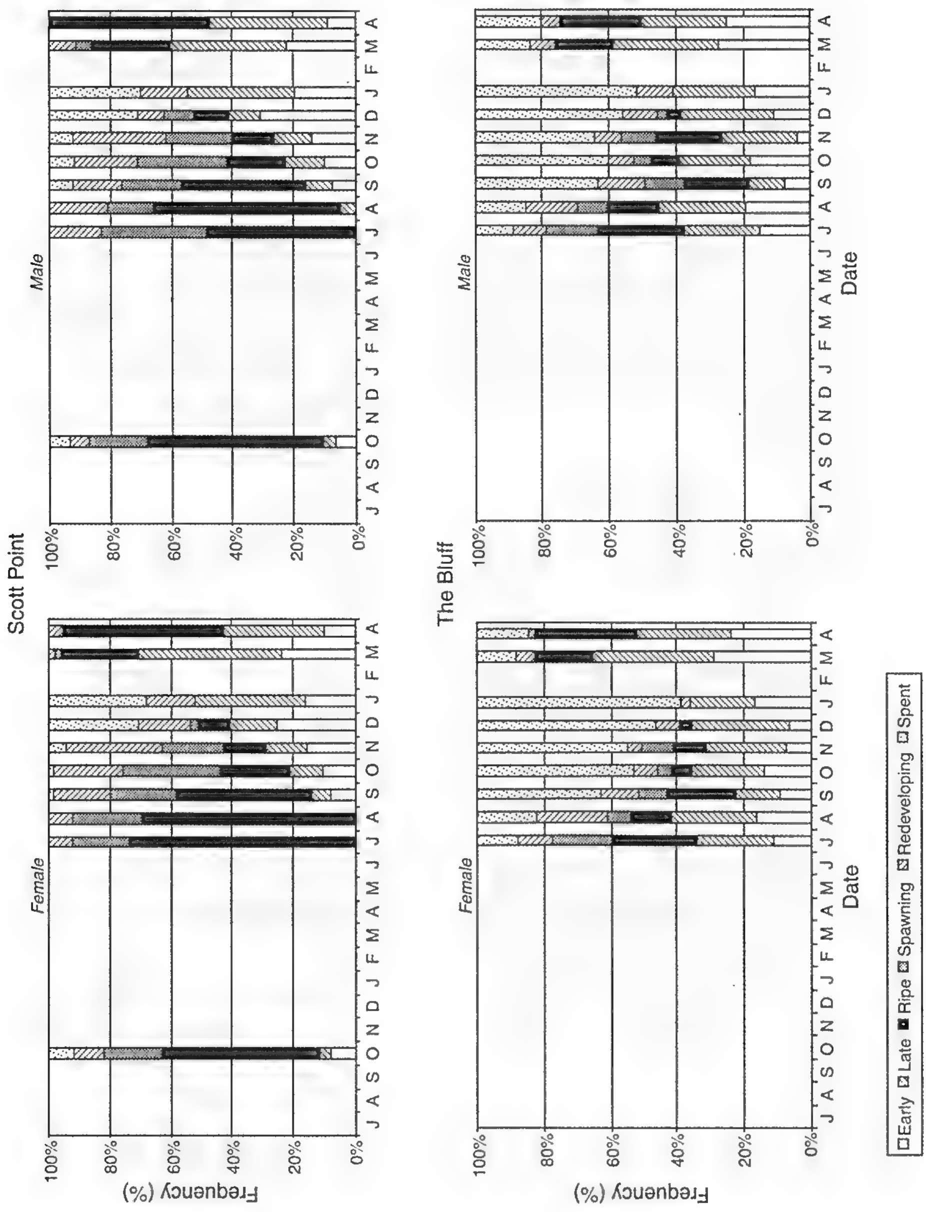

Fig. 7. Frequency distribution of six developmental stages (early development, late development, ripe, spawning, redeveloping and spent) of gonad reproductive state for female and male mussels at two intertidal sites (The Bluff and Scott Point).

mussel populations. Comparisons of gonad indices among the four intertidal populations indicated that The Bluff consistently had the lowest gonad indices (mean (± s.e.) of 146 ± 4 and range of 136–177) during the sampled period, followed by the southern populations of Ungaunga Bay and Tonatona Beach (see previous section) (Fig. 6). Scott Point had the highest gonad indices of all intertidal populations, with a mean (± s.e.) of 217 ± 9 and a range of 180–262 (Fig. 6). Frequency distribution data suggest that the mussel population at Scott Point had the highest percentage of spawning mussels during the reproductive season (March to December) compared to southern intertidal populations, with The Bluff population showing the lowest percentage of spawning mussels (Fig. 7). Also, mussels in the spent developmental stage were more numerous in The Bluff population than the southern populations, whereas Scott Point had the lowest number of spent mussels during the reproductive season (Fig. 7). Repeated-measures MANOVA and profile analyses to test differences in gonad index between southern (Tonatona Beach and Ungaunga Bay) and northern (Scott Point and The Bluff) intertidal sites among 15 months between November 1998 and April 2000 are shown in Table 2. Table 2 also shows the results of single ANOVA tests on paired-date contrasts.

Discussion

The timing and location of mussel spat arrival at Ninety Mile Beach have been previously unpredictable (Jeffs *et al.* 1999). The complexity of interacting physical and biological parameters that affect the green-lipped mussel life cycle have made the study of the ecology of this mussel challenging in the past (Buchanan 1998). Research on the importance of various ecological processes of mussel populations at Ninety Mile Beach is underway and will likely provide evidence of the factors responsible for the high spatial and temporal variability of mussel spat production in the area (A. C. Alfaro, unpublished data). The study of spatial variability in reproductive behaviour among various intertidal and subtidal mussel populations contributes to a better understanding of the timing and magnitude of larval production at various locations along Ninety Mile Beach.

Marked differences in maximum shell length among all intertidal and subtidal populations are likely a result of variations in environmental conditions that regulate feeding rates, such as food supplies, emersion time, hydrodynamic regime, sediment load and temperature (Suchanek 1985; Frechette and Grant 1991; Alvarado and Castilla 1996; Dahlhoff and Menge 1996; McQuaid and Lindsay 2000). Different environmental conditions may also result in different spawning times and duration, as well as more subtle variations in gametogenic cycles (Bayne *et al.* 1983; Nichols 1996; Myrand *et al.* 2000). Experiments conducted by Myrand *et al.* (2000) in the Gulf of St Lawrence revealed distinctive differences in timing and duration of spawning events and in mortality between two populations of blue mussels, *Mytilus edulis*. The two mussel populations originated from the same initial stock but were subjected to different environmental conditions of temperature and water depth around the Magdalen Islands. In this study, comparisons between northern and southern intertidal populations and between intertidal and subtidal populations of Ninety Mile Beach resulted in differences in shell length between months throughout the year but site differences were only significant between intertidal and subtidal sites. Contrast analyses on single date pairs indicated that most of the shell length differences occurred between July and December 1999 for intertidal *v.* subtidal populations and between July and September 1999 for southern *v.* northern populations. However, the mussel shell length information provided in this study can only be used to recognise shell size differences among sites and sampled dates.

The high level of reproductive synchrony observed between female and male mussels in this study has been reported in other *Perna canaliculus* populations (Flaws 1975; Tortell 1976; Buchanan 1998) and in other mussel species (Heffernan and Walker 1989; Villalba 1995; Nichols 1996; Darrigran *et al.* 1999). Despite the great physical distances among populations (from 8–90 km apart) at Ninety Mile Beach, a significant temporal synchrony was also observed in reproductive behaviours among populations over 90 km and both intertidal and subtidal populations (Figs 3–7). This synchrony may imply spawning triggered by some spatially reliable cue, such as changes in water temperature.

These unique temporal patterns in mussel reproduction at Ninety Mile Beach indicate a prolonged spawning season between June and December, which differs from the two spawning periods reported for mussel populations in the South Island, New Zealand (Flaws 1975; Buchanan 1998; Alfaro *et al.* 2001). Conversely, the present study shows clear differences in gonad indices and reproductive cycles among mussel populations within different habitats at Ninety Mile Beach.

Intertidal v. *subtidal populations*

Comparisons of reproductive patterns among intertidal and subtidal mussel populations at Ninety Mile Beach indicate that subtidal populations have consistently higher gonad indices and a higher percentage of ripe and spawning mussels compared to intertidal populations. These trends in reproductive behaviour can be loosely associated with reproductive effort, although more detailed studies incorporating biomass and energy measurements are necessary. Subtidal populations have often been associated with higher productivity than intertidal populations (Suchanek 1978; Thompson 1979; Griffiths 1981; Reusch and Chapman 1997). Furthermore, subtidal mussels tend to have higher growth rates and reproductive efforts owing to the generally prolonged feeding periods and lower stresses from desiccation, temperature fluctuation and predation (Suchanek 1978; Griffiths 1981; Bayne *et al.* 1983; Reusch and Chapman 1997). Thus, mussel populations at subtidal Wizard Rock and Blue House may sustain prolonged reproductive maturity by re-allocating energy from maintenance to reproduction. Another indication of higher reproductive activity is an increase in age and size, often associated with habitats that exhibit more constant environmental conditions (Griffiths 1981; Bayne *et al.* 1983; Petraitis 1995), such as those found at Wizard Rock and Blue House. Mussels from subtidal sites in this study not only had the highest synchronised gonad indices, but also maintained more ripe and spawning mussels through the season. Consistency of parameters in subtidal sites, such as temperature, compared to intertidal sites, also might account for the single but extended subtidal spawning period, with very few spent mussels in the populations until the end of the season. Conversely, rapid temperature changes in the southern intertidal populations at Ninety Mile Beach may be responsible for the distinctively rapid redeveloping and subsequent spawning periods through the season (March to December) for both of these populations (Alfaro *et al.* 2001). The spatial and temporal reproductive differences between intertidal and subtidal populations may emphasise the importance of subtidal populations as major contributors to the spat production at Ninety Mile Beach.

Southern v. *northern populations*

Differences in mussel reproductive behaviour between intertidal habitats at Ninety Mile Beach suggest great variability in overall gonad indices among northern and southern populations. The mussel population at The Bluff had the lowest gonad indices. Although data for this site are not available from July 1999 to April 2000, there is an indication that

this population also had the shortest spawning period among all studied populations. It is difficult to explain why the population at The Bluff had such a low productivity when the nearest population (15 km to the north) at Scott Point had the highest reproductive output at Ninety Mile Beach. Indeed, Scott Point had a consistently high and long spawning period, with low numbers of spent mussels until November. It is possible that less favourable local conditions at The Bluff may contribute to the low reproductive productivity of this population. The Bluff is an isolated patch of rocks in the middle of a long stretch of sandy beach. Thus, the sediment load and wave exposure are high and may be a constant source of stress for mussels surviving on the rocks. Owing to the generally linear coastline of this area, food supplies tend to be irregular and may depend on the northbound nearshore current, with little residence time at The Bluff (A. C. Alfaro, unpublished data). Conversely, Scott Point is located at the northernmost end of the beach, where the mixing of the West Auckland and Westland currents, and the more complex coastal morphology of bays and shallow banks, together create a highly turbulent environment (Stanton 1973). Thus, the combination of dynamic ocean circulation and high delivery and residence time of food particles make the Scott Point area highly productive (A. C. Alfaro, unpublished data). The two southern populations appear to have intermediate reproductive behaviours compared to the Scott Point and The Bluff populations. Although statistical significance was only found for the date factor, contrasts tests indicated that differences between gonad indices were between July and September 1999.

Regional variations in reproductive behaviour have been observed in many mussel populations throughout the world (Bayne *et al.* 1983; Thompson 1984; Jasim and Brand 1989; Nichols 1996). This reproductive variability is believed to be a result of mussels responding to local conditions (Bayne *et al.* 1983; Nichols 1996). Thus, variations in environmental conditions such as water temperature and food availability may be sufficient enough to cause dramatic differences in reproductive behaviour among mussel populations (Hickman and Illingworth 1980; Smit *et al.* 1992; Dorgelo and Kraak 1993; Ram and Nichols 1993; Nichols 1996). For the green-lipped mussel, *Perna canaliculus*, great variations in condition index were found among populations throughout New Zealand, including populations ~36 km apart between Ahipara Bay and Whangaroa Harbour (Hickman and Illingworth 1980). Thus, the variations in reproductive behaviour among all intertidal and subtidal populations at Ninety Mile Beach may contribute, in various degrees, to the highly productive and sometimes spatially and temporally variable spatfall conditions observed in this unique coastal area.

In summary, spatial variability in reproductive behaviour of mussels at Ninety Mile Beach were observed between different populations (between intertidal and subtidal populations and between northern and southern populations), possibly related to varying environmental conditions, such as temperature and food supply. Differences in reproductive behaviour between intertidal and subtidal populations may be a result of the more constant environmental conditions of subtidal populations. As a consequence, subtidal mussels tend to be larger (high growth rates) and have one prolonged spawning period. This spawning behaviour contrasts with the 2–3 spawning periods observed in the two intertidal populations and in Ahipara Bay. Regional differences in Ninety Mile Beach populations are exemplified by the disparate reproductive patterns among northern and southern mussel populations. Low reproductive maturity of mussels at The Bluff may be related to the high stress of sediment loads and irregular food supplies. Conversely, mussels at Scott Point benefit from higher water temperatures and high energy ocean conditions that may ensure high and constant food supplies to these mussel beds. These favourable mussel habitats may

result in the high reproductive activity of mussels at Scott Point and may promote a prolonged spawning season. Mussel populations at Ahipara have intermediate reproductive behaviours compared to those at The Bluff and Scott Point.

Finally, the observed reproductive differences among mussel populations at Ninety Mile Beach suggest that the two subtidal populations at Wizard Rock and Blue House, and the northernmost intertidal population at Scott Point, had the highest reproductive output. This research examined thousands of mussels from an extensive 90-km reach of remote coastline in northern New Zealand. It is the first study to address the potential contribution of intertidal and subtidal mussel populations to the massive spat production of the area, which currently supports the commercial New Zealand mussel industry. Further studies on larval survival, transport and settlement will add important information regarding the temporal and spatial variability of spat arrival to the beach.

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Observations on the feeding behaviour of *Nassarius clarus* (Gastropoda : Nassariidae) in Shark Bay, Western Australia

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Abstract

On a pristine sandflat at Monkey Mia in the World Heritage Site of Shark Bay, Western Australia, lives a single species of nassariid, *Nassarius clarus*. The inner reaches of Shark Bay are hypersaline, i.e. salinity > 60, but at Monkey Mia, waters are metahaline, salinity ranging from 40 to 45. At Monkey Mia, *Nassarius clarus* is attracted to, and feeds on, both autochthonous (bivalves) and allochthonous (fish) carrion. A few records of the species attacking other beach inhabitants, including hermit crabs, which it interacts with at carrion, were also obtained. *Nassarius clarus* is attracted to carrion from a maximum recorded distance of 26 m, reflecting the large scale of such Australian shores. An experiment of disturbing, by scraping, plots of beach sand revealed that *N. clarus* investigates such areas where it feeds on organic detritus and, presumably, damaged meio- and macrofauna. These feeding observations highlight new facets of nassariid behaviour. That is, first, on such pristine beaches, *Nassarius clarus* exploits a range of feeding options, from detritivory, to scavenging and the hunting down of damaged 'prey'. On other shores impacted by pollution and dead fish from fishery by-catches, this opportunism has been masked leading to nassariids being considered near-obligate scavengers. Second, the well-known phenomenon of nassariids departing carrion tainted by damaged conspecifics because, it was thought, of a potential threat of predation upon themselves, is here also seen to occur as soon as the bait was touched by the returning tide. Fish predation on such pristine beaches appears to be a real threat but this aspect of nassariid behaviour has again been masked on polluted and (over-) fished beaches by the near absence of significant predators.

Introduction

Species of the caenogastropod Nassariidae have a virtual global distribution on soft shores and the sea bed (Britton and Morton 1994*a*) and, as more studies are made, the many representatives of the family are revealing a wider than hitherto appreciated adaptive radiation in terms of their behaviours, particularly in relation to feeding.

One of the most well-known nassariids is *Bullia digitalis* (Dillwyn, 1817), which, on exposed South African shores, surfs breaking waves to feed on moribund carrion deposited by the tide (Brown 1971). On north-eastern American shores, *Ilyanassa obsoleta* (Say, 1822) forages on carrion and algae over long expanses of shore, following the tide (Crisp 1969). Other intertidal nassariids, e.g. *Nassarius festivus* (Powys, 1835) in Hong Kong, however, lie buried, awaiting the scent of fresh carrion before they emerge from the sediment to move towards it (Britton and Morton 1992). When *Nassarius reticulatus* (Linnaeus, 1758) was either fed or exposed to food odours, oxygen uptake increased dramatically (Crisp *et al.* 1978), suggesting immediate recognition of carrion. In Queensland, Australia, McKillup and McKillup (1997) reported a nassariid which they identified as *Nassarius dorsatus* (Röding, 1798), ranging widely over the surface of tidally exposed sandflats and foraging actively. Morton and Britton (2003) showed that on a pristine beach in north-western Western Australia, *N. dorsatus* forages actively but only during a narrow window of opportunity at low tide. On the same beach, the sympatric

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Nassarius albinus (Thiele, 1930) behaves in the same manner, as do three other non-nassariid gastropod scavengers. All do so, however, at subtly different states of the tide, i.e. there was a temporal separation in terms of foraging behaviour.

A reconnaisance visit in 2000 to a large intertidal sandflat at Monkey Mia in the World Heritage Site of Shark Bay, Western Australia, showed that only one scavenger (apart from a few hermit crabs), *Nassarius clarus* (Marrat, 1877), was present on the beach and, like *N. dorsatus* at Watering Cove, Burrup Peninsula, Western Australia (Morton and Britton 2003), was only active for a brief period of time over the tidal cycle.

Nassariids occurring in Western Australia have been illustrated by Wells and Bryce (2000). The Australian Nassariidae have also been identified by Wilson (1994) and this author (p. 86–87) stated that *N. clarus* occurs from around Shark Bay, Western Australia, across the northern coastline of Australia and down to Townsville, Queensland, in the east. It is thus tropical and has been recorded from elsewhere in the Indo-West Pacific, e.g. Thailand (Cernohorsky 1984). Nothing of any consequence has, however, been written about the species and Morton and Britton (2003) did not record it from the shores of the Burrup Peninsula in north-western Western Australia.

The waters of Inner Shark Bay (Fig. 1*a*) are hypersaline, especially within Lharidon Bight and Hamelin Pool demarcated by the Faure Sill (Logan and Cebulski 1970), and *Nassarius clarus* does not occur there (personal observations). Outside the sill, however, salinities are metahaline, i.e. salinity between 40 and 56, and, thus, still high in comparison with the oceanic water outside the bay. On the shores at Monkey Mia (Fig. 1*b*), *N. clarus* is the only scavenging gastropod and the first aim of this study was to determine if, like *N. dorsatus*, it is an active forager and if so over what period of the tidal cycle. Coincidentally, any observations of *N. clarus* feeding on other elements of the resident macrobenthic community at Monkey Mia were also recorded as part of this survey (and on a repeat visit in August 2002). One of the problems of putting carrion bait out on some beaches is that gulls become attracted to it quickly and make such field experiments difficult. This was particularly true at Monkey Mia and constrained the second aim of the study, which was to determine over what state of the tide feeding occurs. A third aim of the study, was to attempt to determine over what distance *N. clarus* could travel to arrive at bait and how long individuals fed on it. Finally, a fourth aim was, following on from the observations of Morton and Britton (2002) on *N. dorsatus* feeding on exhumed holothurians following a storm perturbation, to determine if *N. clarus* would investigate any disturbance to its sand habitat.

This is, therefore, a study of a single nassariid occupying a metasaline, pristine beach in Shark Bay and attempts to elucidate aspects of the behaviour that facilitates its colonisation of and singular success on this shore.

Materials and methods

Following the reconnaissance visit in 2000, a research trip was made to the intertidal sandflat south of Monkey Mia within the Shark Bay World Heritage Site in November and December 2001. Over a ten-day period of low tides, visits were made to the beach and a number of observations made and experiments undertaken. First, on four occasions, the beach was visited on a falling tide and the numbers of individuals of *Nassarius clarus* actively foraging was estimated by counting them in 50 randomly thrown 1-m^2 quadrats. This was repeated six hours later on the rising tide, just as the shore was about to be flooded. Thus, a total of 400 one-metre-square quadrats were investigated. During these surveys too, the occasional occurrences of small clusters of *N. clarus* at putative 'prey' were recorded. Second, on five occasions, five haphazardly arranged 25 cm × 25 cm areas of the shore were scraped (with a scraper) to a depth of 2–3 cm to imitate a beach disturbance. Five other, also haphazard, 25× 25 cm^2 areas were outlined on the beach, but

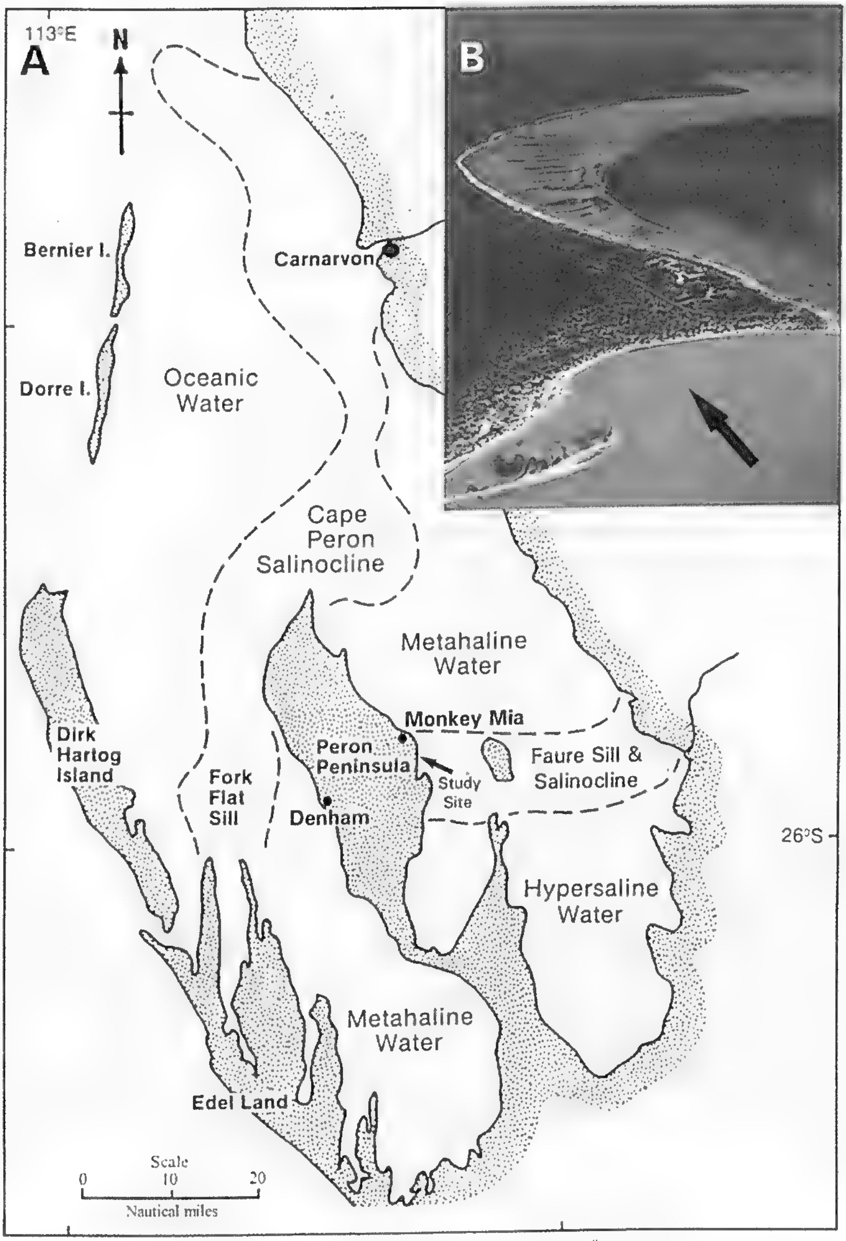

Fig. 1. (*a*) Map of Shark Bay, Western Australia, showing the approximate extents of the various salinity regimes; (*b*) view of the study beach at Monkey Mia, Shark Bay, Western Australia (after Slack-Smith 1990).

not scraped, and these served as 'disturbance' controls. Every individual of *N. clarus* within each plot was recorded at five-minute intervals until no more visits were identified. Third, on two days, five pieces of fresh fish bait, i.e. the pilchard, *Sardinops neopilchardus* (Steindachner, 1879), were staked out at three-metre intervals on the beach at about mid-tide level and at the time of low tide. A stake with no bait was used as a control on each day. The numbers of *Nassarius clarus* individuals arriving at each bait were recorded at five-minute intervals until no more arrived and they had all departed. Finally on five other

Table 1. Records of *Nassarius clarus* attracted to natural prey and fish carrion taken on five separate occasions (*including additional records made in August 2002)

Prey/carrion	Number of *Nassarius clarus*
Fragum unedo (juvenile)	5
Nereis sp.	4
Fragum unedo (juvenile)	5
Fighting hermit crabs	3
**Fragum unedo*	3
**Fragum unedo* (juvenile)	4
**Fragum unedo* (juvenile)	2
**Fragum unedo*	4
**Gnathanodon speciosus* (dead fish)	45

occasions, at the time of approximately low tide, five crushed bivalves *Callista chinensis* (Holten, 1803), were placed in a row, one metre apart facing into a draining area of the shore under the influence of strong offshore winds. Every five minutes, downwind and downflow from the bait, the distance of the furthest individual of *Nassarius clarus* that could be identified moving upstream towards it was measured. The numbers of individuals feeding on the bait were also recorded every five minutes. Checks were also made upwind and upstream from the baits to identify any individuals moving towards them from this direction.

Voucher specimens of *Nassarius clarus* have been lodged at the Natural History Museum, London (NHM 2001–0753) and the Western Australian Museum, Perth (WAM S10823).

Results

Numbers of individuals foraging

On a falling tide, the numbers of individuals of *Nassarius clarus* actively foraging was a mean of 0.89 ± 0.95 m^2. On a rising tide, this was 0.06 ± 0.24 m^2. A *t*-test (d.f. = 199) identified a significant difference ($P < 001$) between receding and rising tides in terms of the numbers of *N. clarus* visible on the beach. At the time of 'just awash' by the rising tide, no individuals could be seen. All had buried themselves and at the times of high tide wading inspections of the beach shallows similarly could not identify any foraging *N. clarus*.

Numbers at natural 'prey'

On four occasions, small groups of *Nassarius clarus* were observed clustered around possible 'prey' (Table 1). On two occasions these were small, exposed *Fragum unedo* (Linnaeus, 1758). On another occasion, four individuals were observed attacking (with proboscis extended) a species of *Nereis*. On a fourth occasion, three individuals were clustered around a pair of fighting hermit crabs. (The beach was visited again briefly in August 2002: at that time four more records of *N. clarus* clustered around exposed *F. unedo* were obtained and some 45 individuals were found consuming a dead fish, golden trevally *Gnathanodon speciosus* (Forsskål, 1775), and arriving at it from downwind and downstream in a line (Fig. 2).

Numbers attracted to 'disturbed' sand

Figure 3 shows the numbers of *Nassarius clarus* attracted to five plots disturbed by scraping and their five controls. Although this experiment was repeated four more times, the results were all comparable. That is, *N. clarus* arrived at the five disturbed plots after 5 min to peak at ~2 individuals·$plot^{-1}$ after 30 min and then to decline to zero after 95 min. In contrast,

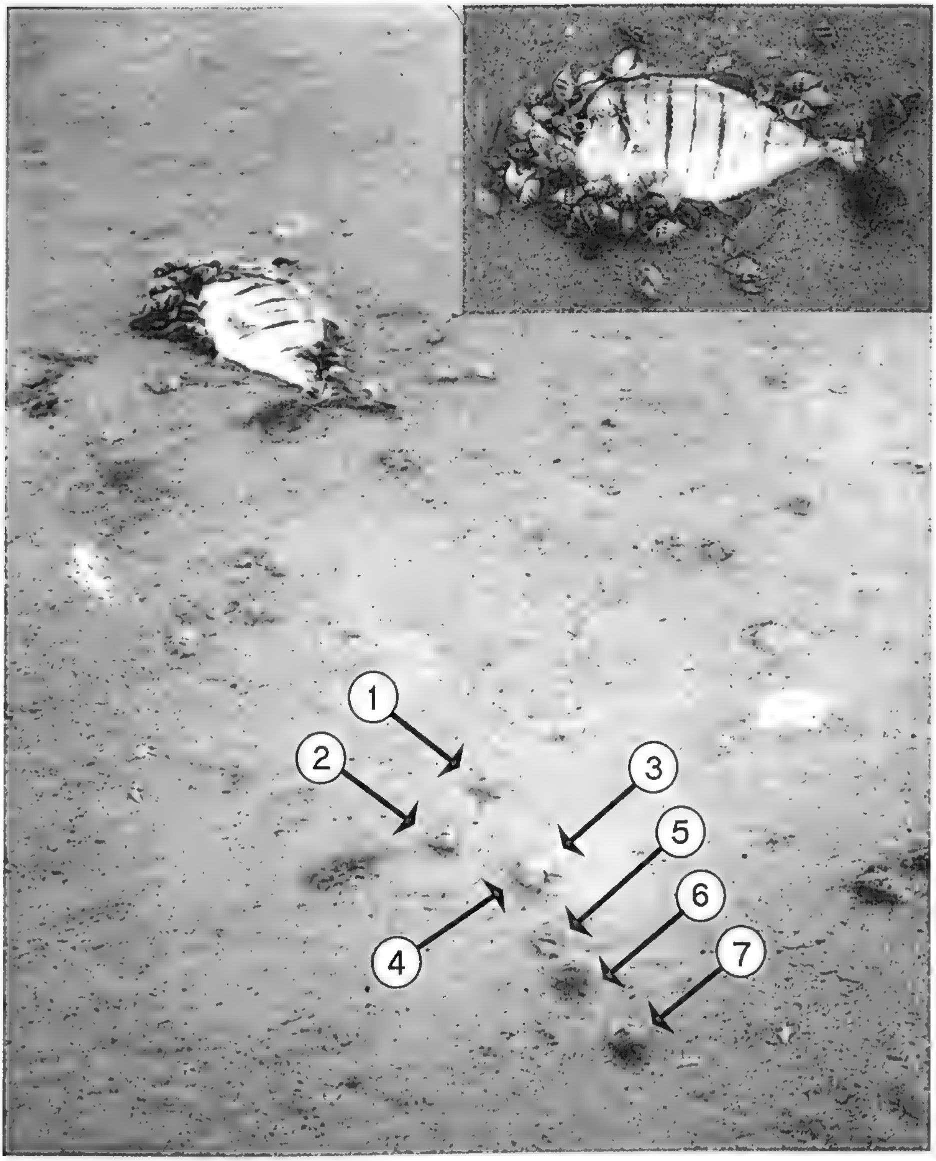

Fig. 2. Individuals of *Nassarius clarus* feeding on (top right) and advancing towards (arrows 1–7) in a line from downward and downstream of a dead fish, *Gnathanodon speciosus*, deposited on the beach at Monkey Mia, August 2002.

only occasionally was *N. clarus* recorded from the control plots. At such times they were either moving across or inspecting the marked perimeters of the plots.

Attraction to staked-out fish bait

The numbers of *Nassarius clarus* attracted to staked-out fish bait on the beach at Monkey Mia, on two occasions, are shown in Fig. 4. No individuals came to control unbaited stakes. On the first occasion, the total numbers of arriving *N. clarus* rose rapidly to 58 within 55 minutes and remained high until >85 min. Thereafter, numbers declined to 22 after

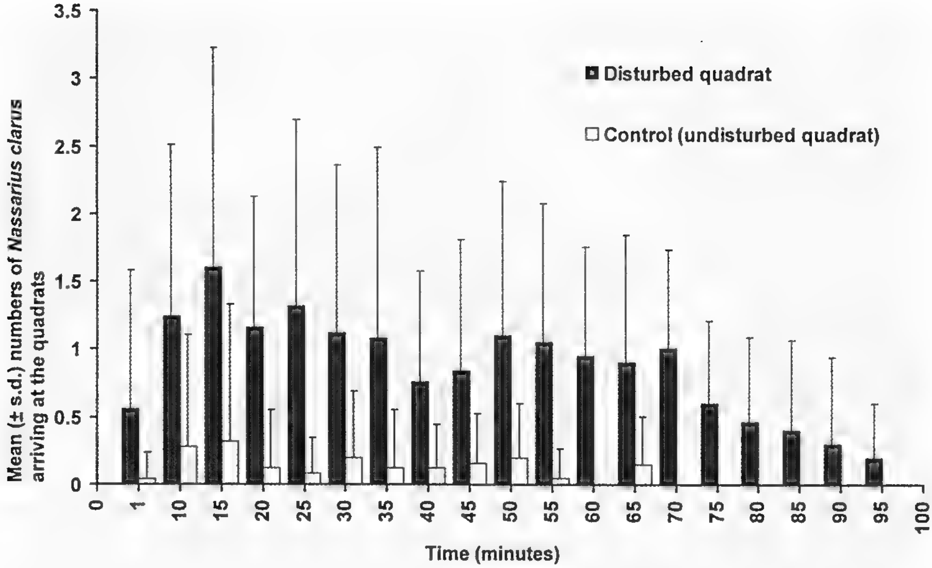

Fig. 3. Mean numbers of individuals (± s.d.) of *Nassarius clarus* arriving at five replicates of 25 × 25 cm quadrats of disturbed sand and an equal number of controls (perimeter-marked only quadrats).

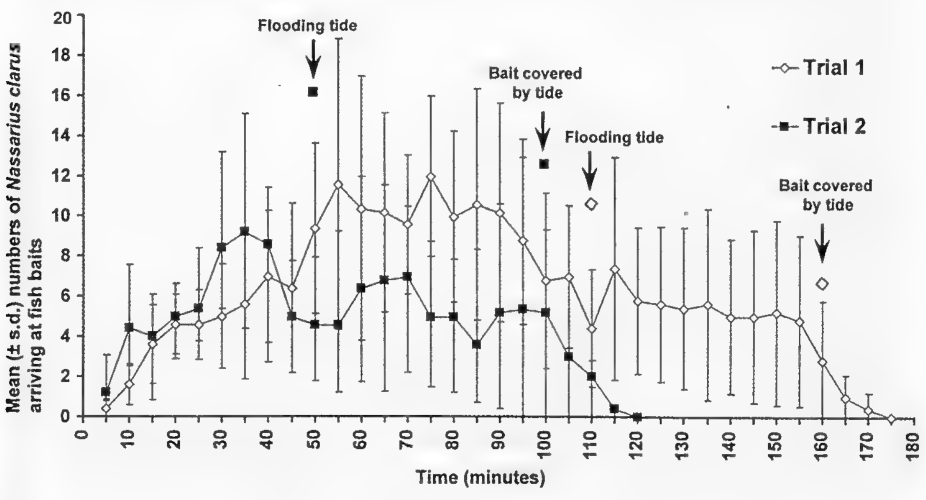

Fig. 4. Mean numbers of individuals (± s.d.) of *Nassarius clarus* arriving at and remaining with five pieces of fish bait staked out on two days on the beach at Monkey Mia, Shark Bay, Western Australia, and at approximately two hours before the return of the tide.

>110 min, this fall coinciding with the rising tide. *Nassarius clarus* remained at the bait (in numbers of ~25), however, until >155 min when the tide covered the bait. At >175 min, no individuals were present. This rapid decline was not accounted for, as described earlier, by individuals arriving at, feeding and then departing the bait, but by *in situ* burial.

On the second occasion, the pattern was repeated. Total numbers of *Nassarius clarus* arriving at the baits rose rapidly to 48 after 35 min and then declined to 23 at >50 minutes. The above decline once again coincided with the advancing tide. Subsequently, however, numbers rose again to 48 at >35 minutes and remained high until >100 min. At this

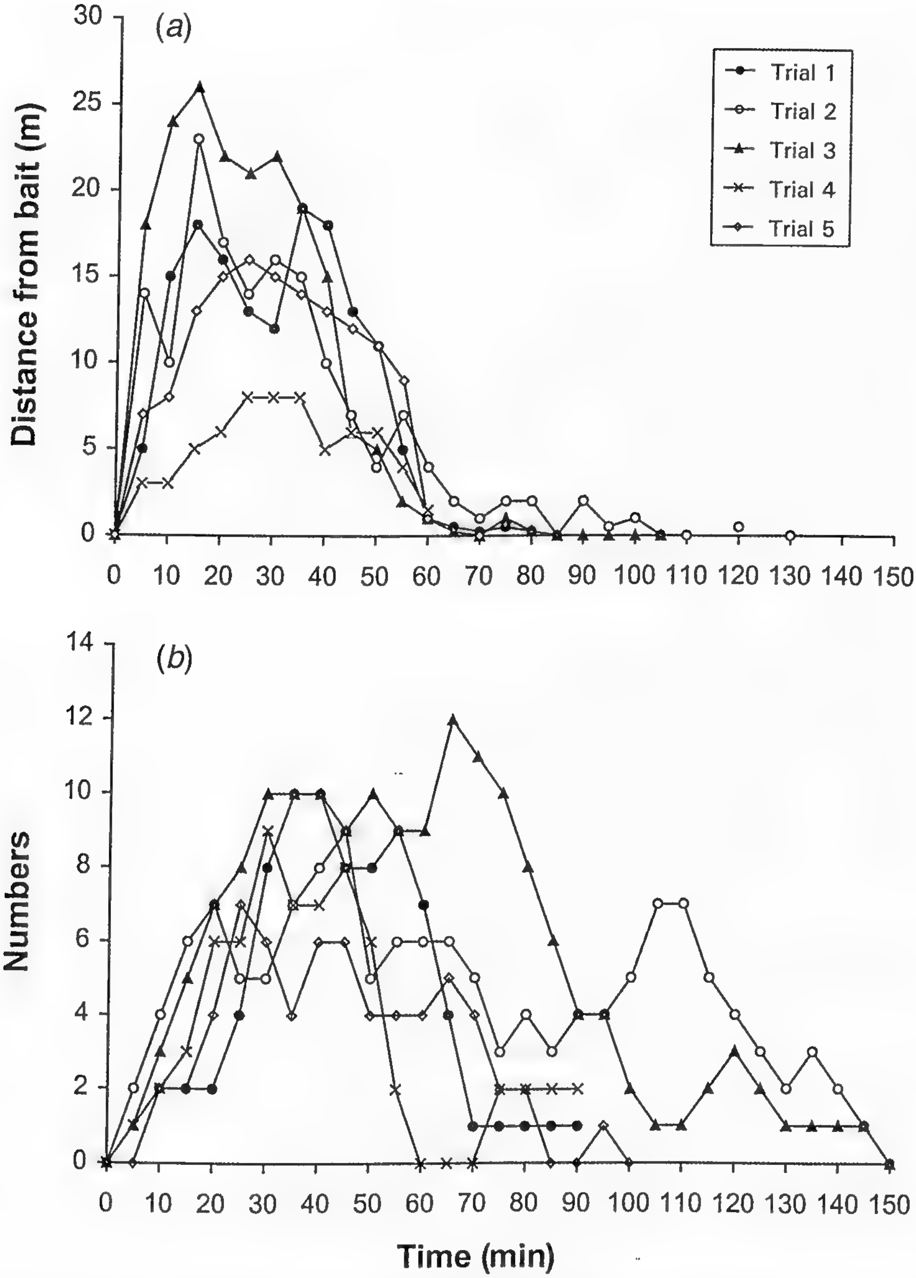

Fig. 5. (*a*) Mean maximum distance from which individuals of *Nassarius clarus* were identified moving towards five pieces of bivalve bait set out on the beach at Monkey Mia, Shark Bay, Western Australia; (*b*) mean numbers of individuals of *N. clarus* arriving at and remaining on the above baits to feed.

moment, the incoming tide covered the baits and within 10 min the numbers of *N. clarus* had fallen from 26 to 0. These individuals had also buried themselves *in situ*.

Attempts were made to repeat the above experiments on three more occasions. On the third, the baits were detected by silver gulls (*Larus novaehollandiae*) and they foiled any further attempt.

Distances and numbers attracted to bivalve bait

It was noted that the silver gulls did not recognise crushed bivalve bait. Thus, five sets of this bait were set out and the numbers of arriving *Nassarius clarus* counted. The greatest distance at which *N. clarus* was seen moving to the bait in the five trials (Fig. 5*a*) rose progressively to between 8 and 26 m after between 25 and 15 min respectively. Numbers declined slowly thereafter and no more arrivals were detected after >80 min. In one trial, this time was extended to 140 min by one or two *N. clarus* intermittently departing and leaving the bait usually into *in situ* buried repose. Beyond the maximum 26-m downstream distance from the bait, other individuals of *N. clarus* were oriented haphazardly, as they were upwind and upstream of the baits.

The numbers of *Nassarius clarus* arriving at the bivalve baits in the five trials is shown in Fig. 5*b*. Numbers peaked at 7 and 12 individuals, respectively, between 20 and 65 min after establishment. Subsequently, numbers generally declined so that by >140 min all had either departed the bait or were buried *in situ*. This burial was again associated with the arrival of the tide but was less obvious because the baits were placed downwind of a flow of draining water. All individuals in all replicates of all five trials had, however, reburied themselves *in situ* before the tide covered them.

Discussion

Britton and Morton (1994*a*) described the Nassariidae as the closest gastropod group in the sea to obligate scavengers. For example, *Bullia digitalis* in South Africa surfs up beaches using a specially modified foot to access stranded carrion (Brown 1971). In the shallow subtidal zone, nassariids are also attracted to carrion (Britton and Morton 1994*b*; Morton and Chan 2001). Both intertidally and subtidally, moreover, the numbers of nassariid individuals and their dominance in the benthic community hierarchy reflect the availability of carrion. On the seabed of Hong Kong, a series of papers (Liu and Morton 1994; Morton 1995; Leung and Morton 1997) showed how the gastropod community has, over time, become dominated mostly by *Nassarius siquijorensis* (A. Adams, 1852) which is also highly tolerant of anoxia (Chan and Morton 1997). Similarly, Hong Kong's soft intertidal shores are dominated by the scavenging *Nassarius festivus* (Britton and Morton 1992; Morton *et al.* 1995). This is also true of shores in southern Australia, so that the degree of hunger expressed by *Nassarius pauperatus* (Lamarck, 1822) on different beaches is related to the availability of food, which also affects egg and egg capsule production and regulates population size (McKillup 1983; McKillup and Butler 1979, 1983).

Most of the above studies have been conducted on beaches that are more (Hong Kong) or less (South Australia) polluted. In these locations, the nassariids identified are lie-in-buried-repose scavengers, which emerge in large numbers when any washed-up carrion is detected. A 'proboscis search reaction' (Kohn 1961) is initiated when carrion is encountered and feeding commences rapidly thereafter. Sometimes, as on the shore of Princess Royal Harbour, Albany, and subtidally at Rottnest Island, both in Western Australia, a number of scavenging species are present and interact with each other to spatially partition the available resources (Morton and Britton 1991; Britton and Britton 1999; Morton and Jones 2003). Most recently, Morton and Britton (2003) reported upon a scavenging gastropod community on a near-pristine beach, Watering Cove, on the Burrup Peninsula, Western Australia. Here, the most surprising observation was that the species involved did not lie in buried repose, but all emerged at some point during the low-tide period to forage for food and demonstrated a temporal partitioning of the available

resources. *Nassarius dorsatus*, in particular, actively pursued, overwhelmed and consumed any damaged animal on the beach.

A final point of interest regarding the above study was that all the gastropod scavengers retreated actively into the sand with the approaching tide presumably because, as was observed, with it came shoals of teleost fishes, bottom feeding rays and small sharks. Morton and Britton (2003) called this beach 'near-pristine', because even in this remote locality, there were some impacts from recreational fishermen. At the World Heritage Site of Shark Bay, the beach at Monkey Mia must be considered 'pristine', or as close to it as is possible today.

On this beach, *Nassarius clarus* behaved much like *N. dorsatus* at Watering Cove on the Burrup Peninsula. That is, on beaches of such large scale, carrion could be detected from long distances, i.e. ~26 m in both of the above cases. Shark Bay is, moreover, especially windy with hot, dry trade winds blowing north-westerly over it, keeping water off the beach and 'streaming' the draining pools. This does, however, assist *N. clarus* to find carrion quickly. On the rising tide, however, the situation changes and because the beach is so flat, water flows up it rapidly, as at Watering Cove. Thus, at both places, although the two species remained feeding at food until satiated, both would retreat into buried repose once the tide began to cover them. Like *N. dorsatus* too (Morton and Britton 2002, 2003), *N. clarus* would investigate any exposed, or damaged possible 'prey' and attack it. *Nassarius clarus* also interacts with hermit crabs, as has been demonstrated for *N. festivus* in Hong Kong (Morton and Yuen 2000), and consumes natural carrion (the present study). This study, however, reveals another aspect of nassariid biology. *Nassarius clarus* will investigate any disturbed area of the beach, presumably because in the sediment there must be particles of detritus and damaged meiofauna. In this situation, *N. clarus* does not evert its proboscis to feed. It does this only with carrion, which may be why experimenters (Britton and Morton 1992) have thought that nassariids feed solely on this material. *Nassarius clarus* appears to feed on detritus without everting its proboscis, as seen in *N. festivus* in Hong Kong (Morton and Chan 2003).

It is not known if *Nassarius clarus*, like other nassariids such as *N. pauperatus* (McKillup and McKillup 1994, 1995), *N. siquijorensis* (Morton and Chan 1999) and *N. festivus* (Morton *et al.* 1995), responds to the presence of damaged conspecifics by fleeing. This behaviour is more understandable now, however, because on pristine beaches such as at Monkey Mia and Watering Cove, any nassariid feeding on carrion at the surface when covered by the tide would be at a great risk of predation from incursing fish. At low tide, when it can be active, *Nassarius clarus* examined disturbed areas, investigated and tackled small exposed components of the normally buried meio- and macrofaunal community and actively sought out allochthonous (fish) and autochonous (bivalve) carrion. From facultative scavenging, therefore, the picture of the nassariid life style may be likened more to opportunism.

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PUBLICATIONS REVIEW

Publications of the Dutch Malacological Society

The Dutch Malacological Society, or Nederlandse Malacologische Vereniging (NMV), has its broad objective in common with the Malacological Society of Australasia – to promote the study of molluscs. It was established in 1934, somewhat earlier than the MSA in 1955. NMV now has about 600 members, which, also in common with the MSA, includes members with a range of interests. Both societies cater for amateurs who collect shells, through fishers and farmers, to those involved in pure and applied scientific research. Both societies undertake activities that include field trips, lectures, conferences, workshops and scientific publication. It is in this last area of scientific publication where NMV is the envy of other malacological societies worldwide, for its range of quality publications addressed to the various segments of its membership. The publications are the scientific journal *Basteria,* the large-format colour publication *Vita Malacologica*, which is issued as a supplement to *Basteria*, and the newsletter *Spirula.*

Basteria

Basteria is the scientific journal of the NMV and commenced in 1936. It is published twice per year in English, with Volume 67 appearing in 2003. It is in A5 size, usually with line drawings and black and white photographs, but Volume 67 contains nine pages of colour illustrations.

Basteria covers a wide range of topics in malacology, including systematics (with check lists), ecology and geographical distribution of all the classes of molluscs, apparently with no limit of geography. As one would expect, European fauna is well represented, as with the paper 'A remarkably rich prosobranch fauna endemic to the French Pyrenees'. In geographical contrast, 'The terrestrial molluscs of Easter Island' deals with a part of the world once remote from Holland, but now only a plane trip away, with the disappointing result that the fauna consists mainly of introduced taxa. Ecological work includes 'Herring gulls learn to feed on a recent invader in the Dutch Wadden Sea, the Pacific oyster', and systematic work includes papers such as 'Studies on the Streptaxidae of Malawi' and 'Four new Diplommatinidae from southern Thailand'.

Although *Basteria* generally does not include many papers on genetics, anatomy and phylogeny, papers are generally accompanied by quality line drawings, and the reproduction of photographs is excellent. Colour plates are sometimes included. However, a recent nudibranch paper includes excellent diagrams of morphology and anatomy, but unfortunately the photos of the living animal are in black and white in contrast to the spectacular colour plates in a monograph on North Atlantic Pectinoidea.

Vita Malacologica

Vita Malacologica is published once per year as a supplement to *Basteria.* Only the first issue, December 2002, has appeared so far, so time will tell whether this approach is successful. As explained in the introduction to the first issue, *Vita Malacologica* has taken over some of the role of *Vita Marina*, publication of which ceased for financial reasons, but is not simply a continuation of that journal under a new name. The casual observer would think otherwise, as *Vita Malacologica* apparently rolls off the same printing press and is

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implemented by the same designers responsible for *Vita Marina;* the page format, printing style and contemporary cover design remain the same, as do the quality paper, the clear and spacious layout and the high-quality colour illustrations.

Vita Malacologica is a journal for the publication of original papers, with the advantage of A4 format and full-colour illustrations. The stated intention is to concentrate on a theme for each issue; themes may be systematic, geographical, methodological, etc. The theme of the first issue is the family Strombidae, although this is not clearly identified anywhere – the reader discovers it by reading the paper titles in the tables of contents. The intention is apparently not to provide a review of the theme, but to simply group together what appear to be *ad hoc* contributions in the area. Hence the issue at hand contains papers on the Stromboidea of north-west Borneo, the distribution of species of *Tibia* in Yemen, and one introducing two new Indo-West Pacific strombid genera.

Publishing a supplement to a scientific journal with a different format and content and giving it a separate title is an unusual approach. However, in the realm of making specialist scientific publications viable, everything (as in love and war) is allowable. With the ever-increasing number of scientific journals and newsletters competing for a fixed pool of readers, and ever decreasing budgets of libraries and museums, any new approach to publishing is worth a try.

Spirula

Spirula is the newsletter of the Society, appearing six times per year. It contains the usual items for a malacological newsletter – club news, short articles, observations and field trip reports – but, in addition, has regular sections that are a service to the international malacological community, both amateur and technical.

The observation articles in *Spirula* are themselves substantial contributions, such as items on the invasion of muricids into French oyster beds and the appearance of an Indo-West Pacific keyhole limpet in the Mediterranean. These items are in Dutch, but an abstract is given in English.

Each issue of *Spirula* contains a taxonomically arranged list of newly described shelled mollusc species-group taxa (apparently) worldwide. The list includes the name, geographic locality and the literature reference. Accompanying this is a summary of general taxonomic publications, also arranged by family. Both provide very useful resources to keep up to date with current developments.

Of more general interest, the newsletter contains sections on new books, covering a range from very technical to general interest, and a regular section of molluscs on stamps. The coverage of NMV publications is indeed comprehensive!

Further information about the Dutch Malacological Society can be found at www.spirula.nl.

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Authors and Titles

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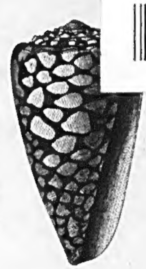

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